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THE ZOOLOGICAL SOCIETY OF LONDON

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THE PROCEEDINGS OF THE ZOOLOGICAL SOCIETY OF LONDON

THE TRANSACTIONS OF THE ZOOLOGICAL SOCIETY OF LONDON

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REPORT OF THE PATHOLOGIST FOR THE YEAR 1959

BY

R. N. T.-W.-FIENNES, M.A., M.R.C.V.S.

Zoological Society of London

[Accepted 14th March 1961]

An analysis is given of the causes of death and main infecting organisms amongst 494 mammals, birds, reptiles and amphibians which died at the Regent's Park Gardens during the year 1959. A description is given of the *post mortem* findings in the more interesting cases.

Progress reports are given on items of research into animal diseases carried out during the year.

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GENERAL

As forecast in the previous year's report, that now presented appears in a somewhat different form. All *post mortem* work is being recorded in a punch card system, and this gives easy analysis of statistical data. Such data are transferred to a standard series of tables, which it is proposed to maintain unaltered for purposes of comparative reference over the years. The possibility of transferring former records to the new system for purpose of analysis is under consideration. Should this be undertaken, an easy further step will be to present an analysis of data extending to 1908.

One difficulty over compilation of health statistics in a zoological collection lies in the increased susceptibility of newly-imported creatures to accident and disease. Apart from the fact that they are more susceptible to " township " diseases than animals which have been acclimatized, it is evident that they are often in a state of " stress " and for this reason more liable to infection and injury. In past years, attempts have been made to overcome this difficulty by arbitrarily distinguishing between those animals which have been resident in the Gardens for six months and over, and those which have been resident for less than six months. This method shows obvious deficiencies, to overcome which *post mortem* material is now numbered in two series, a " red " series for newly-imported animals and a " black " series for acclimatized animals. The decision as to whether any case should be included in the " red " or the " black "

series is made according to the history. For instance, a python which has been resident for nine months but has never fed will be included in the " red " series, whereas some other animal dying in less than six months of a cause not associated with acclimatization or travel factors will be added to the " black " series.

Whereas previously all cases have been presented for statistical purposes together with a supplementary table for the non-acclimatized creatures, in future statistical work will be based only on the " black " series ; the " red " will be presented only for comparative purposes. In this way, results will be more truly representative of the causes of death amongst *established* populations of captive animals of different species.

The development of the Society's new animal hospital and the provision of full veterinary, pathological and bacteriological services has had a marked effect on the statistical picture. Deaths from avoidable infectious causes have diminished and the total death rate has declined. For this reason, statistical data will be of greater value in revealing the natural pathological states which develop in different species, and less of a catalogue of the various infections to which they are prone. This state of affairs has been accomplished partly by more rapid and more reliable diagnosis in the sick animal, partly by more rapid and more efficient treatment rendered possible by the better facilities available, and partly by greater attention to general hygiene and to examination and surveys of animals or groups of animals to discover and eliminate carriers of disease.

On the research side, such *ad hoc* investigations as have been necessary have been undertaken. In addition, the policy mentioned in the previous year's report of encouraging workers with mutual interests has been pursued with considerable success.

AUTOPSIES

With few exceptions, autopsies are performed on all animals which die in Regent's Park. Results of this work are given in Tables 1 to 4. Table 5 gives

Table 1—Analysis of deaths occurring amongst acclimatized animals at Regent's Park during 1959.

	1958	1959					
		1st Qtr.	2nd Qtr.	3rd Qtr.	4th Qtr.	TOTAL	Nos. at 31.12.59
Mammals	140	46	38	33	30	147	722
Birds	232	69	76	44	65	254	1,496
Reptiles & Amphibia	96	23	15	20	35	93	400
TOTAL	468	138	129	97	130	494	2,618

a summary of results derived from newly-arrived animals which had not become acclimatized. Table 6 gives a summary of specimens examined during the year from living animals. Little comment is required on the material contained in these tables. The deaths amongst the collections continue at a satisfactorily low level.

Table 2—Analysis of the causes of death amongst the main classes of animals.

	Mammalia	Aves	Reptilia etc.	TOTAL
Senility	3	26	6	35 (7%)
Inanition	1	1	10	12 (2·5%)
Injury, etc.	19	41	8	68 (14%)
Specific Diseases	0	2	0	2
Septicaemia	9	2	5	16 (3%)
Tuberculosis	6	6	0	12 (2·5%)
Mycosis	3	12	0	15 (3%)
Parasitic	5	2	12	19 (4%)
Circulatory	2	13	3	18 (3·5%)
Alimentary	44	70	18	132 (27%)
Respiratory	33	28	16	77 (16%)
Urinary	0	28	8	36 (7%)
Reproductive	3	8	7	18 (4%)
Locomotor	1	0	0	1
Nervous	1	1	0	2
Endocrine	0	0	0	0
Skin	0	0	0	0
Metabolism	3	9	0	12 (2·5%)
Neoplasms	1	5	0	6
Other causes	13	0	0	13 (2·5%)
TOTAL	147	254	93	494

The diagnosis of senility would not be acceptable in normal hospital practice; but where animals whose age is known have shown no definite cause of death at autopsy, the term may be used cautiously in zoological practice to indicate a trend towards longevity and away from preventable disease.

There now follow descriptions of the more interesting cases that have been encountered during the year :—

CASE HISTORIES

A. *Whipsnade Park*

Assistance was sought from the Pathologist at Regent's Park in two cases of disease outbreaks at Whipsnade Park, which occurred during the year under review. They were :—

1. An outbreak of Piroplasmosis due to *Nuttallia* (*Babesia*) *equi* in Grevy's zebras.

2. An outbreak of malignant catarrh in Père David's deer.

Table 3—Analysis of the causes of death amongst the main Orders of Mammalia.

	1	2	3	4	5	6	7	8	9	10	TOTAL
Senility	0	0	3	0	0	0	0	0	0	0	3
Inanition	0	0	0	0	0	0	0	1	0	0	1
Injury, etc.	4	0	7	0	4	0	3	0	1	0	19
Specific Diseases	0	0	0	0	0	0	0	0	0	0	0
Septicaemia	1	0	0	1	2	0	3	2	0	0	9
Tuberculosis	0	0	3	0	1	0	2	0	0	0	6
Mycosis	0	0	1	0	0	0	0	0	2	0	3
Parasitic	0	0	1	0	4	0	0	0	0	0	5
Circulatory	0	0	1	0	1	0	0	0	0	0	2
Alimentary	8	1	5	0	16	0	4	3	7	0	44
Respiratory	5	2	3	1	11	1	6	0	4	0	33
Urinary	0	0	0	0	0	0	0	0	0	0	0
Reproductive	0	0	0	0	3	0	0	0	0	0	3
Locomotor	0	0	0	0	0	0	0	0	1	0	1
Nervous	0	0	1	0	0	0	0	0	0	0	1
Endocrine	0	0	0	0	0	0	0	0	0	0	0
Skin	0	0	0	0	0	0	0	0	0	0	0
Metabolism	1	0	0	0	1	0	0	0	1	0	3
Neoplasms	0	0	1	0	0	0	0	0	0	0	1
Other causes	3	0	0	1	3	0	2	0	4	0	13
TOTAL	22	3	26	3	46	1	20	6	20	0	147

1. Primates 22
2. Insectivora 3
3. Carnivora 26
4. Pinnipedia 3
5. Rodentia and Lagomorpha 46
6. Perissodactyla 1
7. Artiodactyla 20
8. Edentata 6
9. Marsupialia 20
10. Other Orders

TOTAL 147

B. *Regent's Park*

There was no epidemic of any kind amongst the animals at Regent's Park during the year. The following is an account of the more interesting cases investigated *post mortem*.

Mammalia

i. Primates

Two deaths of monkeys occurred during the first quarter of the year as a result of dysentery caused by *Shigella sonnei*.

A Senegal galago died as a result of haemorrhage from a deep eroding gastric ulcer. Two weeks prior to death the tail was injured and this was subsequently amputated. Two weeks later the galago had died with gastric ulcer and symptoms of shock. The sensitivity of galagoes to injury of the tail has previously been noted. The history of this case is of especial interest as indicating a possible connection between the gastric ulcer and a condition of "stress".

Smoky Woolly Monkey. This was the female of a pair of woolly monkeys and she died of pneumonia. It had been hoped that the pair which had been

together for about a year would breed. At *post mortem*, however, both ovaries were found to be cystic and there was some thickening of the uterine wall.

ii. Carnivora

Tiger. A tiger collapsed and died during the first stage of anaesthesia after apparently submitting readily to restraint. Death was due to rupture of the liver, a circumstance which must give rise to speculation since there was no history of undue struggling and the animal apparently did no more than turn itself over in the anaesthetic box. The liver was enormously swollen due to congestion with blood. It seems likely that the excitement of the preliminary stage of anaesthesia triggered a state of shock resulting in congestion of the abdominal organs, including the liver.

Table 4—Showing identifications of infecting agents in *post mortem* specimens.

N.B. Inclusion in this list does not necessarily indicate that the organisms were the cause of death.

		Mammalia	Aves	Reptilia & Amphibia	TOTAL
	Cocci	11	4	0	15
	Corynebacterium	0	0	0	0
	Acid Fast	6	6	0	12
	Pasteurella	1	3	1	5
	Salmonella	8	5	1	14
BACTERIA	Shigella	2	0	0	2
TOTAL	Coliforms, etc.	12	28	4*	44
	Brucella	0	0	0	0
	Anaerobes	2	1	0	3
	Spirochaetes	0	0	0	0
	Actinomyces	4	0	0	4
	Fungi	1	9	1	11
	Viruses	0	0	0	0
	Cestodes	3	3	6	12
HELMINTHS	Nematodes	2	5	10	17
TOTAL	Filaria	0	0	0	0
	Trematodes	0	0	0	0
	Sporozoa, etc.	0	0	0	0
	Trypanosomes	0	0	0	0
PROTOZOA	Amoeba	1	0	6	7
TOTAL	Coccidia	1	0	0	1
	Balantidium	0	0	0	0
	Other Protozoa	2†	0	0	2
	Ecto-parasites	5	0	0	5
	TOTAL	61	64	29	154

* Two of which were deaths from *Proteus hydrophilus* in snakes.

† Giardiosis in Lesser Egyptian Gerbils.

Table 5—Analysis of causes of death amongst unacclimatized animals.

	Mammalia	Aves	Reptilia, etc.	TOTAL
Senility	0	0	0	0
Inanition	0	2	61	63
Injury, etc.	14	7	1	22
Specific Diseases	0	0	0	0
Septicaemia	0	0	0	0
Tuberculosis	0	0	0	0
Mycosis	0	0	0	0
Parasitic	4	0	1	5
Circulatory	0	0	0	0
Alimentary	10	6	0	16
Respiratory	1	4	1	6
Urinary	0	2	1	3
Generative	0	0	0	0
Locomotor	0	0	0	0
Nervous	0	1	0	1
Endocrine	0	0	0	0
Metabolism, etc.	0	0	0	0
Neoplasms	0	0	0	0
Other causes not ascertained	24	0	85	109*
Decomposed	6	2	133	141
TOTAL	59	24	283	366

* Mostly reserved for morphological studies.

Table 6—Showing the results of bacteriological, parasitological and biochemical tests on clinical specimens from living animals.

Mammals	358
Birds	58
Reptiles	42
TOTAL	458

Lion (No. 1). The following case is another instance of the death of a large carnivore apparently associated with a large shock component. The lion was slightly mauled by the lioness about the face and at the time of *post mortem* there was a slight oedematous but uninfected reaction of the site. The lion had been brought to the Hospital for treatment and was for a day or two confined in a crush box. He was then transferred to one of the dens. At first he ate small quantities, mostly pigeons, but eventually refused food completely. He lay quietly until he became so weak from inanition that he could not take food and had to be destroyed. He had been treated with chloromycetin in the form of palmitate emulsion in the water. He continued to drink up to the time of his death.

During life the case was puzzling because it suggested an exacerbation of either chronic hepatitis or nephritis. There was, however, no oedema or ascites except that of the face and at *post mortem* only small areas were found in the axilla or the groin. At *post mortem*, an apparent hepatitis was found with irregularity of the surface of the liver suggestive of cirrhosis. The kidneys were normal. Upon histological examination the liver was found to be slightly cirrhotic and there was some focal necrosis. It was grossly congested with both blood and bile, the latter indeed was under considerable pressure, so that when the gall bladder was punctured it squirted into the air. The bile duct was, however, not blocked and the duodenum contained bile. The following signs were found at autopsy which suggested a condition of shock :—

1. The liver—extreme congestion.

2. The lungs—the characteristic atalectasis, with emphysematous patches, due to collapse of the vascular tree.

3. The vascular system—there was congestion of the venous system especially in the abdomen. There was dilation of the right heart. There were haemorrhages of the leaves of the mitral valve.

4. The adrenals—the right adrenal was the size of a medium-sized hen's egg. The various zones were indistinguishable and exhausted. The size of the organ was due chiefly to haemorrhage in the form of an organized clot about one inch in diameter. The other gland was not haemorrhagic but showed the typical changes of exhaustion.

This lion was supposed to have been about 19 years old but the body did not show marked signs of ageing except that the testes were atrophied.

Lion (No. 2). This lion was painlessly destroyed because of advanced senility and unfitness for exhibition. The *post mortem* revealed chronic cirrhosis of the liver. Throughout the lung there were fibrous nodules the size of golf balls.

Both cirrhosis of the liver and chronic emphysematous changes of the lungs are very common in ageing lions. The etiology is not understood. The fibrous nodules in the lungs of this lion were not neoplastic, but may be regarded as post inflammatory granulomata.

Indian Leopard Cat. This leopard cat had been under treatment for some time because of actinomycosis. Externally there was a red fibromatous swelling on the gum of the right side : the bone of the jaw was unaffected. There were a few nodules in the lungs the size of marbles. The cat was destroyed as unsuitable for exhibition. Culture from lungs and pus of jaws yielded actinomyces, probably *A. israeli*.

Northern Lynx. A lynx had been diagnosed as a positive tuberculous case, and received treatment. The treatment had not proved effective and it eventually died in coma. On *post mortem* there was no sign of active tuberculosis, but the liver on histological examination proved to be affected with large tuberculous granulomata. The organ was very cirrhotic and regeneration attempts had led to proliferation of bile ducts.

Malayan Civet. A civet which had only been resident in the Gardens for about three months, died suddenly without previous symptoms. On *post*

mortem, the pericardium was distended with a large blood clot and with serum. Examination showed the presence of an aneurysm of the aorta. This appeared to be the result of arteritis.

Pallas's Cat. This cat, as in the last case, was a recent arrival, and the body was received in an advanced stage of inanition. Both the small and large bowel were packed with numerous nematodes of different species.

Striped Hyaena. One of the striped hyaenas, a female, which had been resident in the Gardens since June 1952, died as a result of tuberculosis. There was a suppurating abscess on the left side of the root of the tail. There was severe tuberculous peritonitis with adhesions. There was pyothorax and the pleural cavity contained about a gallon of purulent fluid. There was also tuberculous pericarditis. In addition there were abscesses in the cortices of both kidneys.

Tibetan Wolf. The wolf was affected with acute yellow atrophy of the liver together with haemorrhagic enteritis and peritonitis. The condition was found to be associated with infection with paracolon bacilli.

Kinkajou. A kinkajou suffered from generalized tuberculosis affecting the lungs, liver and spleen. Situated at about the middle of the large intestine there was a very large ulcerating tuberculous nodule. Masses of acid-fast bacilli were easily found in all organs which contained tubercles.

Crab-eating Raccoon. This raccoon had deep bites with lacerations to the left posterior axilla and to both feet. The right foot was much swollen. The injuries were, however, of a minor nature, and death occurred as a result of shock. The adrenals were in an exhausted condition and the general signs were those associated with shock.

Striped Skunk. This skunk suffered from a duodenal ulcer. This was a deep eroding ulcer about 1/8 in. in diameter. There was a second ulcer of similar type in the ileum. At these points the gut appeared to have become twisted and death was due to a strangulated bowel. Nothing especially noteworthy was found from bacteriological examination. *Bacillus coli* was, however, present in the duodenum, a site which is unexpectedly high in the intestinal tract for the presence of this organism. The lower gut contained *Pseudomonas aeruginosa* containing salmonella antigens. This flora probably indicates a condition of chronic bowel dysfunction which may have contributed to the development of the ulceration.

Polar Bear. The polar bear ' Ivy ' was the mother of the young female polar bear ' Brumas ' which had been born in the Gardens, and died during 1958 at the age of eight years. This polar bear was known to be about twenty years old, and there were signs of senility in the body. The lungs showed evidence of bronchiectasis and there was considerable peribronchitis. Both kidneys were small and sclerotic indicating nephritic changes of long standing. In the gut there were numerous large ulcers in the colon although the remainder of the intestinal tract appeared to be normal. Two large ascaris worms were found in the large bowel. Bacteriological examination revealed the presence in the large bowel of the intermediate Providence group of organisms which

carried salmonella A antigens. Death was ascribed to long-standing degenerative changes in the lungs and kidneys associated with senility.

Himalayan Black Bear. This bear was killed *in extremis* after a short but violent illness. The alimentary tract showed acute haemorrhagic enteritis with the outlet of the bile papilla blocked by swollen mucous membrane. The liver was a golden-yellow colour, somewhat mottled. The edges were thickened and the whole organ much swollen. It was very friable and portions easily broke off as if it had been boiled. The gall bladder was swollen with undischarged bile which was thick, viscid and green in colour. The lungs showed gangrenous nodules at the terminations of the bronchi indicating that fluid had been aspirated into them during the last few days of life. Since no attempt had been made to dose the animal this must have arisen from choking. The diagnosis was death from hepatitis associated with haemorrhagic enteritis.

Bacteriological examination showed that *Pseudomonas aeruginosa* was present in the gut and liver and also in the kidneys. Histological examination of the kidneys revealed that there was a hyaline necrosis affecting chiefly the proximal tubules ; this is a type of nephritis typically associated with pseudomonas infection. This case is of interest owing to the increasing evidence of the association of pseudomonas with disease in some captive animals. The young polar bear ' Brumas ' mentioned in the last paragraph died as a result of infection with this organism and a manatee, too, died from pseudomonas septicaemia.

Baikal Seal. Four baby Baikal seals were received from Russia, all of them unweaned. One of them failed to feed and died one week after arrival. Death proved to be due to septicaemia associated with the presence of *Salmonella typhimurium*. There was a small quantity of food material in the large intestine and it is assumed that this creature had attempted to feed on a piece of food material which had decayed and was contaminated.

Common Seal. This seal had been resident ten years in the Gardens having been received as a pup. It showed no definite signs of ageing but the blubber was thinner than normal. Death was due to broncho-pneumonia. The seal's circulatory system was normal, but the liver showed an advanced degree of cirrhosis of uncertain origin.

Southern Elephant Seal. The seal died from degeneration of the heart with gross passive congestion.

iii. Rodentia

Guinea Pig. One Guinea pig appears to have died as a result of dysentery arising from *Balantidium* infection of the gut. This is reported since it is a somewhat unusual condition in Guinea pigs.

Orange-rumped Agouti. This was an accident death resulting from two puncture wounds in the region of the scapulae. On incision, the whole of the back from the base of the neck to the lumbar regions was found to be infested with " flesh fly " larvae. The tissues were in a state of liquefaction, and black. The diagnosis was toxaemia from myiasis, death being due to accidental and parasitic causes.

Two Lesser Egyptian Gerbils. These gerbils, in common with many imported, died of enteritis. The enteritis was caused by giardia. This is thought to be the first observation of giardia in gerbils and may possibly account for the losses of these animals, such as commonly occur when they are newly imported. The treatment for giardia is so simple that it might be recommended to treat all newly-arrived animals.

Capybara. The old capybara died of tuberculosis. This appears to be a common disease in these animals.

European Hare. A hare, which had started to settle down following capture, an unusual event in hares, was disturbed accidentally and died of shock. It is recorded here because certainly ascertained deaths from shock followed by *post mortem* are somewhat rare and of importance.

iv. Artiodactyla

Impala. This impala had been resident two years in the Gardens, having been born in the menagerie. Death was due to broncho-pneumonia there being two large areas of complete consolidation in each lung. Cultures showed that the causal organism was *Corynebacterium pyogenes*.

Arabian Oryx. This oryx suffered from a small but abraded wound of the right hip. This had become infected and there was a form of gas gangrene. The organisms isolated were *Fusiformis necrophorus* together with aerobacter. This was, therefore, a simulated gas gangrene since true gas gangrene organisms were not present.

Lord Delamere's Bushbuck. This bushbuck died of pneumonia with associated pneumococci. This is a somewhat unusual organism to find in these animals and therefore worthy of record.

Eland. The eland died of tuberculosis. The extent of infection in lungs and other organs was very severe indeed.

Llama. This was a case of paratyphoid due to *Salmonella typhimurium*.

v. Perissodactyla

Malay Tapir. A Malay tapir was imported during October and died after one month's residence in the Gardens. It was a young animal and in good condition. It died as a result of pneumonia with solid patches in both lungs. Cultures revealed the presence of haemophilus, *Pseudomonas aeruginosa* and Friedlander's pneumobacillus.

vi. Xenarthra

Seven-banded Armadilloes. Two armadilloes died and *post mortem* was made. These were discovered to be suffering from pasteurellosis. Sensitivity tests were done on the organism and the appropriate treatment was given by the Veterinary Officer to the other armadilloes which were also sick. The treatment proved successful and there were no further losses.

vii. Edentata

Tamandua Anteaters. Two newly-arrived tamandua anteaters died as a result of salmonellosis.

viii. Marsupialia

Bennett's Wallaby (No. 1). This wallaby died as a result of haemorrhage arising from an ulcer of the duodenum. This most unusual case was examined by the Pathologist at St Mark's Hospital for gastric diseases where the existence of a typical duodenal ulcer was confirmed. Bacteriological examination of the gut contents revealed the presence only of *Staphylococcus albus*.

Bennett's Wallaby (No. 2). This wallaby died as a result of nocardiosis which had affected not only the left mandible but had penetrated upwards to cause mycotic inflammation of the nasal cavity and sinuses. In addition, the roof of the left side of the cranium had several localized areas of inflammation affecting the meninges.

Red Kangaroo. Examination had been made of faeces from this kangaroo for some weeks before death. By a new technique recently-developed cultures of nocardia were isolated from the samples. There were bony lesions in the jaws such as are usually associated with this infection. At *post mortem*, however, it was ascertained that death was due to pneumonia caused by nocardiosis. The right lung was a caseous mass firmly adherent to the chest wall. The remainder of the lung tissue was interspersed with pneumonic patches. Nocardia was cultured from pneumonic areas in the lungs.

Opossums. A pair of opossums was received in the Gardens and the female shortly produced eight young. Only one of these survived, but the conditions under which the other babies died are of interest. The one opossum was always strong and healthy. All the others were found at *post mortem* to be weakly and under-nourished and they suffered from anaemia and rickets. It is evident that the mother had been able only to feed one of her young and the others died as a result of inanition.

Squirrel-like Flying Phalanger. This animal died as a result of a perforated duodenal ulcer. The history is of some interest since there is a possible association of this condition with a state of stress. The hind quarters and the root of the tail were partly denuded of hair and skin and encrusted with scabs. The condition was caused by the animal constantly biting itself. Examination for parasites was negative. It appears, however, that there was some source of irritation in this area and that the animal was in a state of stress.

Aves

Black-footed Penguins. Three black-footed penguins were lost during the year as a result of inanition arising from unknown causes.

Finsch's Bird of Paradise. This bird died of embolism of the right lung, and rupture of the right auricle. It has been well known for some time that birds of paradise after importation are prone to die from a cerebral condition leading to paralysis of the hind limbs. Studies made on some of them were reported last year, *Erysipelothrix rhusiopathiae* being isolated from the brain in four cases. This organism is very inclined to cause capillary embolism and it is possible that the death of this bird may have been a sequel to infection.

RESEARCH

General

In previous years surveys have been made into diseases of snakes, of the monkey colony in relation to incidence of infection with tuberculosis and dysentery and on the incidence of enteritic diseases amongst the bird population.

During the present year, the health of the animals in the collections has been good and there has been no necessity for any such surveys to be undertaken. Dr Neal of the Wellcome Foundation has continued his work into the diagnosis and cure of amoebiasis in snakes and will be reporting on this in due course. This work can only be done in the spring when grass snakes are available and it is being continued during the spring of 1960 when it is hoped to complete it.

The Animal Welfare and Husbandry Committee has been interested in the question of mycotic infections of birds (Aspergillosis), and work on this has been conducted in collaboration with Mr P. G. Austwick, Mycologist at the Ministry of Agriculture Veterinary Laboratories, Weybridge. There is nothing at present to report as a result of this work.

Nocardia infection remains a source of anxiety in kangaroos and wallabies. The allied actinomycotic infections appear to be common in some of the smaller Felidae such as fishing cats. Investigations have been pursued with a view to earlier diagnosis. It was found possible to demonstrate the presence of Nocardia and Actinomyces in stool samples by the same technique as that used for demonstrating tuberculosis. This is done by digesting as much faeces as possible in antiformin or acid phosphate solutions at incubator temperatures, by then centrifuging and making cultures on media such as Loewenstein as is done for Mycobacterium. These cultures are readily obtained and the Nocardia or Actinomyces is easily identified. In two cases in which assistance has been sought from external sources, it was possible to diagnose Nocarida infection in sick wallabies before diagnostic clinical signs had appeared. Sensitivities of the organism to antibiotic drugs were determined and early treatment resulted in complete cure of the animals. Complete cure of this disease in kangaroos and wallabies is a rare event and this is a demonstration of the importance of early diagnosis and correct determination of the most active antibiotic for purposes of therapy.

Much time was spent during the year on the re-organization of records and in preparations to make card indexes covering the world literature and past records of the Society going back for many years. In addition, we have continued to augment our library of coloured photographs and to build a collection of histological material from both normal and diseased organs. It has also been possible to give greater histological coverage to normal *post mortem* work.

With the reduction in routine work it has been possible to devote more time to the development of fundamental research in collaboration with external workers.

Investigations into the comparative incidence of cardiovascular diseases.

A most satisfactory relationship has developed during the past three years with a group of scientists at the Royal Free Hospital, London. The persons

involved are Professor K. R. Hill, Professor of Pathology, Royal Free Hospital, Dr A. C. Symons, Clinical Cardiologist, Dr Kathleen Rigg, Research Cardiologist, and Dr Rodney Finlayson, Research Pathologist. For nearly three years the hearts and arteries of virtually all animals dying in the Zoological Gardens at Regent's Park, including birds, mammals and reptiles, have received expert and detailed investigation. The results have been prepared for publication and presented at a Scientific Meeting of the Zoological Society after the conclusion of the year under review (June, 1960).

Professor Hill is also conducting a detailed investigation into the comparative pathology of the livers of the majority of animals presented for *post mortem*, Results are not ready for publication.

"*Stress syndrome*"

In the Pathologist's report for the previous year the belief was expressed that the "stress" component was an important factor in the pathology of captive wild animals. Certain recurring anomalies in the *post mortem* picture were explained as being ascribable to shock consequent upon a state of "stress". An account was given of the signs of this condition as seen *post mortem* and some reference was made to the observable signs during life.

During the year under reference work on this condition has continued. It is not, however, possible here to give more than a general account of the lines which this is taking. The main difficulty has been to confirm by experimentation an hypothesis based on observational work. Biochemical facilities are not yet available in our laboratories and experimentation on animals is not undertaken. It has, however, been possible to form a research team with Dr Raymond Greene and Dr Bird. With their collaboration and help it has been possible to overcome some of these difficulties. The lines along which this work is developing will now be briefly described :—

1. The condition of all adrenal glands, both macroscopically and microscopically is being examined to test whether the condition of these glands supports the diagnosis of shock or "stress".

2. A survey has been made of all deaths occurring at Regent's Park during the past two years from injury and violence in order to determine what percentage of these have been ascribed as being in major part due to a shock factor. The results of the survey are given in tabular form in Appendix I. The results show that no less than 43 per cent of such deaths have been in greater part ascribed to shock factors including, in some cases, gastric and duodenal ulcer. In some animals, stress appears to be easily induced in cases of injury to the tail and a note has been made where such injuries have appeared to be the prelude to a state of "stress" and death arising from it.

3. Consideration has been given to the development of specific tests to determine either the existence or the extent of the "stressed" state. In man comparative blood eosinophil counts are often taken to indicate a state of "stress". It is not possible to use this method in the animals with which we deal. Difficulties are attendant on catching them and in drawing blood, and to do this in any case is likely to induce a state of "stress" and thus to vitiate the result. The possibility of analysing adrenal glands for ascorbic acid

APPENDIX I

ANALYSIS OF ACCIDENTAL DEATHS IN MAMMALIA—1958—1959 (inclusive)

Animal	INJURY			SHOCK CONDITION				TOTAL
	Severe Injury	Injuries from Fighting	Wounds with Generalized or Localized Infections	Shock without Injury	Slight Injury leading to Shock	Shock associated with Operation	Slight Injury associated with Gastric or Duodenal Ulcer	
PRIMATES (inc. Tree shrews)	3 (all Tree shrews)	4	0	0	5 (2 with injury to tail)	0	1 (tail injury)	13
CARNIVORA Lion, tiger, leopard, sand cat, serval, otter, ocelot, marten, raccoon, polar bear, sloth, bear	6	0	0	2 (both otters)	2 (lion and raccoon)	3	0	13
RODENTIA Squirrel, mouse, rat, gerbil, cavy, hare	4	0	1 (hare)	1	3	0	0	9
RUMINANTIA Sheep, goat saiga, oryx, blackbuck	4	3	1	0	0	0	0	8
MARSUPIALIA Wallaby, rat, kangaroo, phalanger, opossum	0	0	2	1 (short-tailed wallaby)	1 (rat kangaroo)	0	2 (wallaby, phalanger)	6
TOTAL	17	7	4	4	11	3	3	49
	28 = 57 per cent			21 = 43 per cent				

content was also considered likewise to be rejected for the time being. It was eventually decided that the only feasible method would be to make corticosteroid analyses of the urines of "stressed" and "unstressed" patients. This required the provision of metabolism cages which were not available. One was, however, obtained and came into use early in 1960. At the time of writing (June 1960) significant results have been obtained and these will be reported at a later date.

Osteodystrophies of New World monkeys

An account was given in the previous year's annual report of researches into this disease. The opinion was then expressed that the so-called rickets of these animals was of renal origin and thus *osteodystrophia fibrosa cystica*. Investigations into the histology of the kidneys of affected cases have continued and some parathyroid glands have been examined. This work is being pursued and a number of blood analyses have been made. We have continued to collaborate in this with Professor G. Cunningham of the Royal College of Surgeons and we are now also being assisted by Professor Dent of the University College Hospital Medical School, an acknowledged expert on bone pathology. It is hoped that some definite results will be available in due course.

A TAXONOMIC ACCOUNT OF THE LARVAE OF SOME BRITISH SYRPHIDAE

BY

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[Accepted 11th October 1960]

(With 117 figures in the text)

This paper is a study on the taxonomy of the immature stages of the Syrphidae. Special attention has been paid to the groups of the family which do not have aphidophagous larvae. The external morphology of a typical saprophagous larva and comparative chaetotaxy of the larvae is described and new sensilla are recorded. The changes in appearance at puparium formation are described. The external features of the third instar larvae and puparia of forty-six species are described and notes on their biology are included. A key for the identification of these and some other larvae is given. A major revision of the classification of the family is proposed as a result of the study of the larvae. This recognizes only two subfamilies, Syrphinae and Milesiinae. Most of the present subfamilies are reduced to tribal status but the Cheilosiinae prove to be heterogenous and its species fall into other groups.

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INTRODUCTION

There are no general accounts of the morphology or taxonomy of syrphid larvae, other than for some of the aphidophagous species. This paper is an account of the external morphology and biology of forty-six non-aphidophagous larvae. Keys are included for the identification of these and other larvae. The phylogeny of the family is discussed and a revision of the classification is proposed.

The Syrphidae is one of the largest and most sharply defined families of the Diptera, both as adults and larvae. The larval habits are varied. They are saprophagous, phytophagous, or predacious, and a few are scavengers in the nests of social insects. The saprophagous habit appears to be the primitive

one. In spite of the varied habits of the larvae, all except *Mesogramma* have one feature in common ; the posterior pair of spiracles are always fused together.

The external features of several larvae have been described from time to time. Most of these descriptions are insufficient for taxonomic purposes. The only general taxonomic work is that of Heiss (1938) but this is restricted to some non-aquatic forms from Illinois. Heiss has produced a key that runs across the natural classification of the family and so it is of little use except for those species included in it. Bhatia (1939) and Scott (1939) describe and illustrate the larvae of several aphidophagous species. Scott includes a key to the puparia of twenty-seven species. Lundbeck (1916) gives rather vague descriptions of the larvae of several species and gives some information on their biology. Hennig (1952) lists many references and gives some rather unsatisfactory keys. Some aspects of the morphology and biology of *Volucella* have been described and illustrated in the monumental work of Künckel d'Herculais (1875). Krüger (1926), in a lengthy account, describes some aspects of the biology and morphology of several species. Other references are mentioned in the text where appropriate.

The taxonomy of the family has been discussed by several authors and the subject is reviewed in detail by Goffe (1952). Most of these classifications have been based on adult characters. The recent classification by Hull (1949), which has been followed by Coe (1953 a), recognizes fourteen subfamilies. Hull considered his classification, which is entirely on adult characters, to be based on phylogeny. Goffe, however, believed the trends cited by Hull to be incorrect, a view which is supported by this paper. Goffe also produced a new classification with two subfamilies based primarily on larval types. His subsequent divisions were based on adult characters.

MATERIALS

In most instances the larvae, collected by searching in the field, had to be reared to adults before they could be identified. Some were reared from eggs laid by captive females. Mature females caught near their oviposition sites often lay eggs readily. *Volucella* larvae have been successfully recovered and reared from the nests of wasps after anaesthetization with trichlorethylene.

The mature larvae have very thick cuticles and are not killed satisfactorily by immersion in a fixative. For good fixation with the larvae in an extended condition it is necessary to inject the fixative with a hypodermic syringe. It is sometimes desirable to kill the larvae with the anal papillae protruded. This can be done by a modification of the method of Gäbler (1930). The larvae are killed in water at 50°C and are then held between finger and thumb with the anus showing. The larva is squeezed and the body behind the anus bent dorsally, simultaneously the anal fold should be pulled back with a blunt instrument. Afterwards the larvae should be fixed by injection.

Cuticular structures have been rendered more visible by the use of carbol-fuchsin stain. Gurr's water mounting medium has been successfully used for preparations of the spiracles.

GENERAL FEATURES OF THE LARVA

The larvae of the Syrphidae pass through three instars before pupation. The first two instars have most of the features of the third although the spiracles are less developed. The third instar larva of a typical saprophagous species is blunt ended anteriorly and more or less cylindrical, the posterior end is usually tapering and ends in a longer or shorter telescopic breathing tube bearing the posterior spiracles. In the Syrphinae and some other species there is no telescopic breathing tube and the spiracles are sessile on a more rounded posterior end. The larva has the usual three thoracic and eight abdominal segments of cyclorrhaphous Diptera. The head is very reduced and is only represented externally by the pair of bilobed antenno-maxillae, the mouth, and the connecting cuticle. There is a small fleshy lobe just above the mouth and below the antenno-maxillae which will be referred to as the dorsal lip.

The prothorax is large and as wide or nearly as wide as the other segments. The anterior surface folds abruptly inwards to meet the cuticle of the head. Dorsally this fold is very pronounced and is referred to as the anterior fold of the prothorax. On the ventral side of the prothorax there is a fleshy lobe either side of the mouth forming a pair of lateral lips. These are in the same relative positions as the prolegs on the next segment. Prolegs may be present on the mesothorax and first six abdominal segments. On the dorsal side of the first abdominal segment there are two circular patches with a different pubescence. It is through these that the pupal spiracles will be thrust after pupation. The anal fold is near the anterior edge of the ventral side of the eighth abdominal segment.

The eighth and sometimes the seventh abdominal segments are variously modified and may be much narrower than the rest of the body. In some species there are laterally three pairs of fleshy protruberances or lappets at the end of the body. These are usually derived from the eighth segment but in *Helophilus pendulus* two, and in *Mallota cimbiciformis* all three, are derived from the seventh segment. The eighth segment is sometimes long and tapering (*Pocota*, *Sphegina*) or sometimes modified into a distinct tail (Eristalini, *Sericomyia*). These modifications are associated with the posterior spiracles which are sometimes borne on a longer or shorter breathing tube. The elongation of the eighth abdominal segment forms a protective sheath into which the breathing tube can be retracted.

The cuticle is unpigmented and transparent but as it thickens in the third instar it becomes whitish and opaque. It is covered with a pubescence of fine microtrichia or spinules. The spinules are sometimes replaced by pimples. The size of the spinules varies slightly in different parts of the larva. They tend to be longer on raised folds, especially laterally and posteriorly. On the anterior fold of the prothorax the spinules are usually larger, stouter, recurved and lightly sclerotized. There may also be large spines present.

a. Chaetotaxy

The term chaetotaxy is used here in a rather wide sense. Strictly it is applicable only to the arrangement of setae and has been so used for some

nematocerous larvae. In the Syrphidae setae of the type found in the Nematocera are not present. Instead there is a segmental arrangement of sensilla, each with one to many fine setae around it. The number and arrangement of these sensilla corresponds quite closely with the setae of *Aëdes* and other mosquito larvae (Christophers, 1960). It is therefore proposed to use the term chaetotaxy to cover the arrangement of sensilla in syrphid larvae.

The sensilla tend to be borne on papillae, which are usually larger posteriorly. The number of setae on each sensillum is not constant and may vary within a species, but in those species which have only one or two setae the numbers are constant. The setae vary in length and are generally longer toward the posterior end of the body. A sensillum can also have long and short setae associated with it. Some of the forms are shown in Fig. 1.

Various terms have been used previously for these or similar structures, which for various reasons are deemed unsuitable. These include : sensorium (Imms, 1942), *organes sensoriales* (Keilin, 1915), sensory papilla (Bhatia, 1939), segmental seta (Heiss, 1938), and *Papillen* (Hennig, 1952).

The chaetotaxy of the syrphid larvae has received some attention from previous authors, but none of their accounts is complete. Hennig (1952) has a map for *Volucella* species but has not distinguished blind papillae from those with sensilla, nor are all the ventral sensilla recorded. Krüger (1926) has incomplete maps of the chaetotaxy of an abdominal segment of several species, but he has correctly recorded the blind papillae of *Volucella*. Heiss (1938) following Metcalf (1913) has named three dorsal and three lateral sensilla as : median, dorsal, dorso-lateral, lateral, posterior ventro-lateral, and anterior ventro-lateral ; these correspond with D1, D2, D3, L1, L3, L2, respectively in the present system. Heiss has omitted all the ventral and ventro-lateral sensilla.

The positions and nomenclature of the sensilla are shown in Fig. 2. The positions of the spiracles are also included as they provide a useful landmark. Reference to a particular sensillum is made thus : MsL1, where Ms refers to the segment (mesothorax) and L1 to the particular sensillum of that segment. Most genera exhibit partial or complete fusion, or loss of some of the closely approximated sensilla. The minimum number of distinct sensilla retained on a typical abdominal segment is nine or ten, distributed as three dorsal, three lateral, one ventro-lateral, and two or three ventral.

The chaetotaxy of the last abdominal segment (A8) has not been fully resolved. If it is a modification of the pattern found on the other abdominal segments and not derived independently from an older pattern, it is possible that the sensilla correspond in the following way :

7, 8, 9 with V1, V2, V3
1, 2 with VL1, VL2
3 with D4
4, 5, 6 with L1, L2, L3.

This correspondence does not appear close in some species with reduced numbers of sensilla, but presumably these reductions are more recent than the formation of the sensilla pattern of the eighth abdominal segment. The

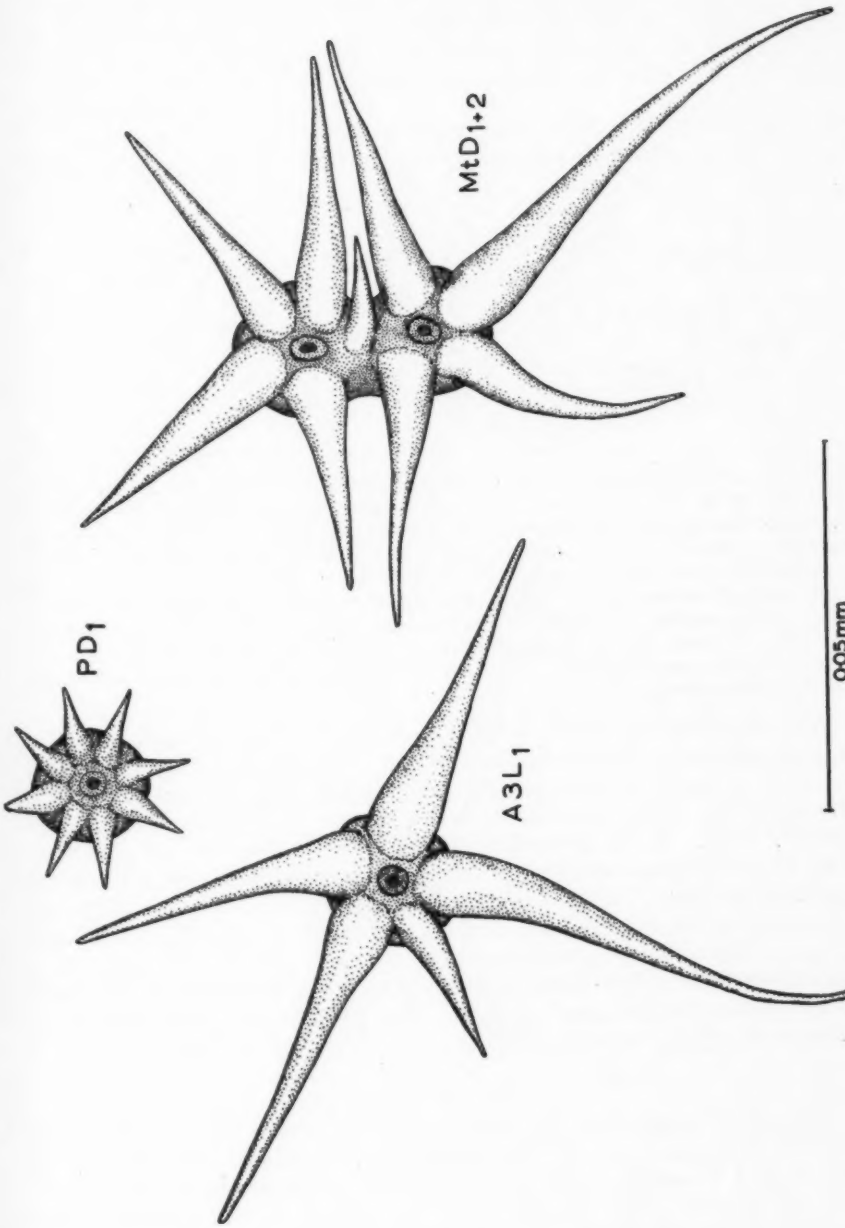


Fig. 1—*Sphegina clunipes* F., Third instar larva ; some of the forms of the segmental sensilla. See Fig. 2 for explanation of nomenclature.

Eristalini have an extra sensillum on this segment that is not found elsewhere in the family. In its present position it appears to be an addition to the ventral group. It has not been numbered. A full appreciation of the chaetotaxy of the last segment will not be possible until much more is known about the chaetotaxy of other dipterous larvae.

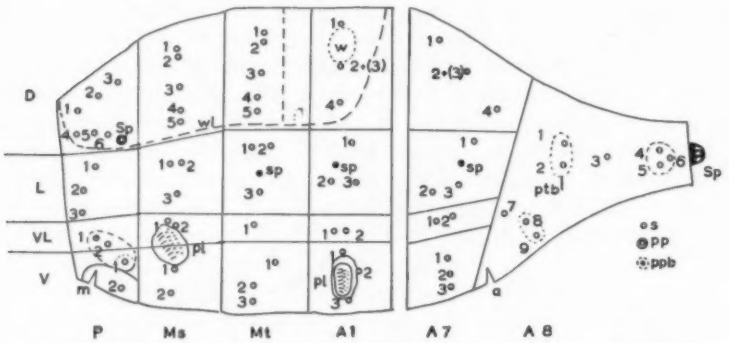


Fig. 2—Map of the chaetotaxy showing the nomenclature of the sensilla. The arrangement of the sensilla on the left side of the first four and last two segments is shown. The abdominal segments 2–6 are not shown as the arrangement is the same as on the first and seventh abdominal segments. a, anal slit ; A1, A7, A8, first, seventh and eighth abdominal segments ; D, dorsal ; L, lateral; m, mouth ; Ms, mesothorax ; Mt, metathorax ; P, prothorax ; pl, proleg ; pp, long papilla bearing sensillum ; ppb, " blind " papilla without sensillum ; ptb, fleshy protuberance or lappet bearing sensilla ; s, sensillum ; Sp, functional spiracle ; sp, nonfunctional spiracle ; V, ventral ; VL, ventro-lateral ; w, area of differentiated cuticle forming the window in puparium through which the pupal spiracles will be thrust ; wl, line of weakness after puparium formation bounding the opercula.

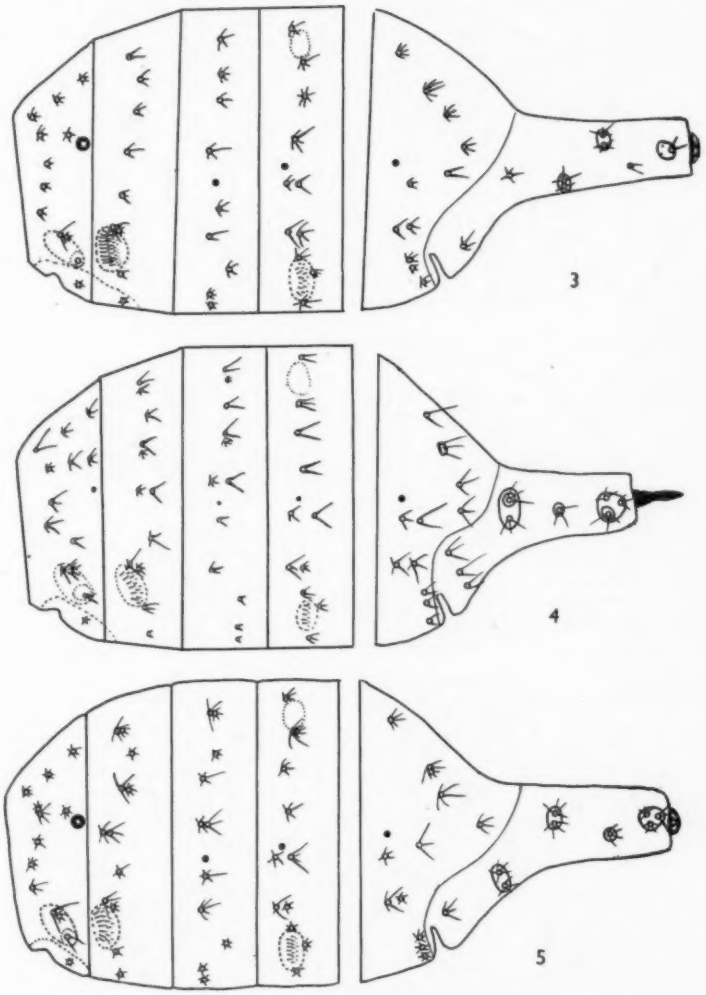
The distribution of sensilla in various genera is shown in Figs. 3–18. The greatest number of distinct sensilla is found in *Chrysogaster* (Fig. 4). Partial reduction is found in *Sphegina* (Fig. 5), *Callicera* (Fig. 17) and part of the Milesiini (Figs. 9, 16) where most of the closely approximated sensilla are partially fused. In the Eristalini (Fig. 3), *Neoascia* (Fig. 8), and *Brachyopa* (Fig. 10) all the paired sensilla are completely fused with the exception of the ventro-lateral pair. *Volucella* (Figs. 6, 7), *Rhingia* (Fig. 11), *Cheilosia* (Fig. 15), *Eumerus* (Fig. 13) and *Merodon* (Fig. 14), and the Syrphinae (Fig. 18) all have complete fusion of all paired sensilla and *Eumerus* and *Merodon* have lost a ventral sensillum. A ventral sensillum has also been suppressed by the fusion of the prolegs in *Callicera*. *Microdon* (Fig. 111) shows a reduction in the number of sensilla, with apparent fusion of the lateral two L2 and L3.

b. Prolegs

One pair of prolegs may be present on the mesothorax and each of the first six abdominal segments. The mesothoracic prolegs, when present, are between the VL and V1 sensilla, whereas those on the abdomen are between the V1 and V3 sensilla. This suggests that the thoracic and abdominal prolegs belong to different series. Prolegs are absent on the prothorax and are replaced by a pair of fleshy lobes either side of the mouth in the same series as

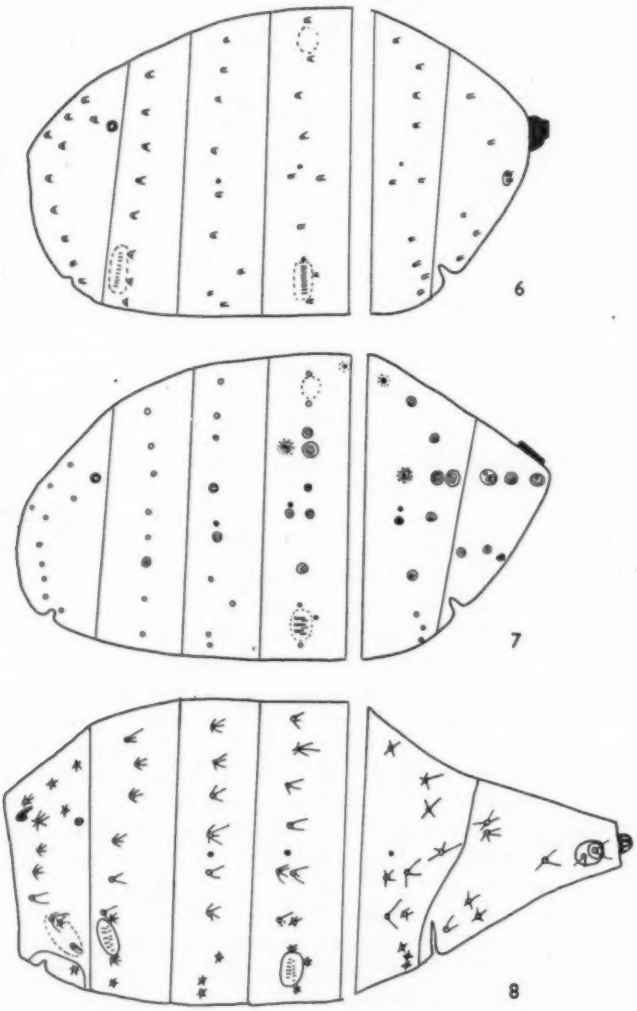
the prolegs on the mesothorax. There are never prolegs on the metathorax. Hinton (1955) describes the thoracic prolegs as on the prothorax, but their relationship to the chaetotaxy and the presence of the prothoracic lobes shows that they belong to the mesothorax. This does not alter Hinton's distinction between predacious and non-predacious larvae as the prolegs are still very close to the mouth.

The prolegs bear claw-like spines or crochets. These are usually arranged in several rows. Those in the first row, the primary crochets, are the longest.



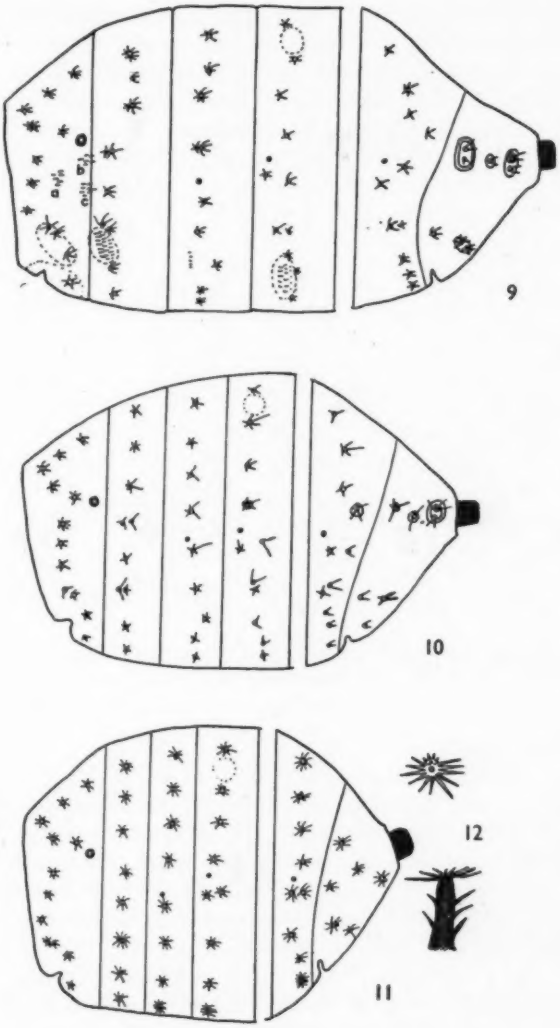
Figs. 3–5—Chaetotaxy maps of the third instar larvae of : (3) *Eristalis sepulchralis* L., (4) *Chrysogaster hirtella* Loew, (5) *Sphegina clunipes* Fall.

Those of the next row, the secondaries, may be stouter but they are always shorter. Other rows have distinctly smaller crochets. Usually the crochets point backwards and slightly outwards but on the last two or three pairs of prolegs the crochets may be more outwardly directed and usually on the posterior pair at least some are anteriorly directed. In some larvae there is a row of anteriorly directed, small, crochet-like spines, just anterior to the sixth abdominal pair of prolegs, but separate from them.



Figs. 6–8—Chaetotaxy maps of the third instar larvae of : (6) *Volucella inanis* F., (7) *Volucella pellucens* L., (8) *Neoascia podagrica* F.

The prolegs of each segment are distinct except in *Callicera* where each pair are partially fused. In the *Volucella pellucens* group the mesothoracic prolegs are absent, a feature that is normally associated with predacious larvae (Hinton, 1955). *Chrysogaster* has a gradient of proleg development, prolegs are larger anteriorly and the sixth abdominal prolegs are without crochets. Crochets are absent altogether in several different groups, and in these the

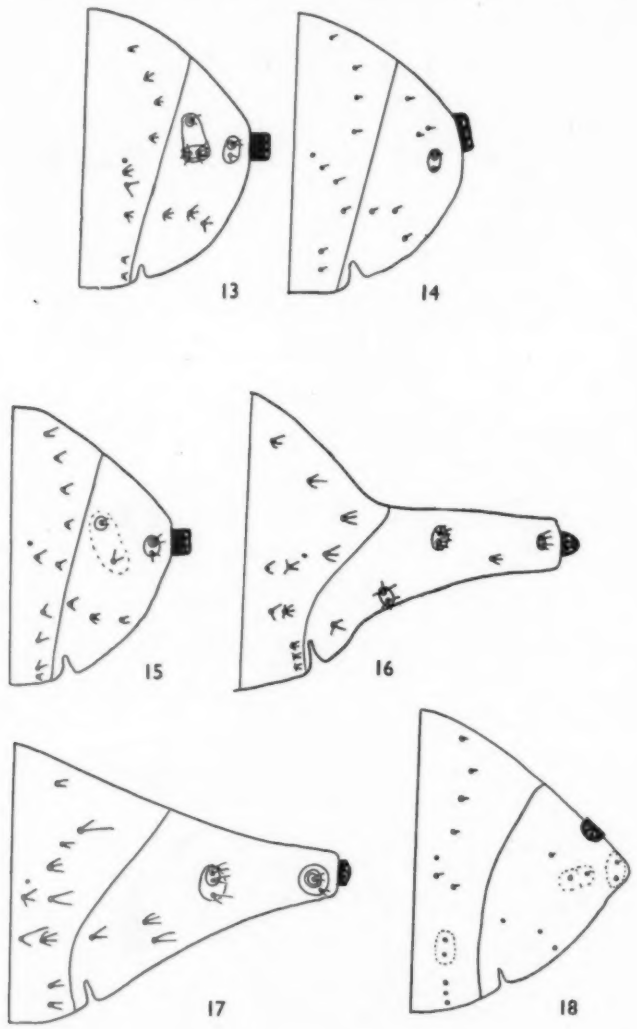


Figs. 9–12—Third instar larvae ; (9–11) chaetotaxy maps of : (9) *Syritta pipiens* L., (10) *Brachyopa* sp., (11) *Rhingia campestris* Meig. ; (12) end and side view of a posterior sensillum of *Rhingia campestris* Meig.

prolegs are also vestigial or absent (Syrphinae, Microdontini, the *Brachyopa* group, and the phytophagous species).

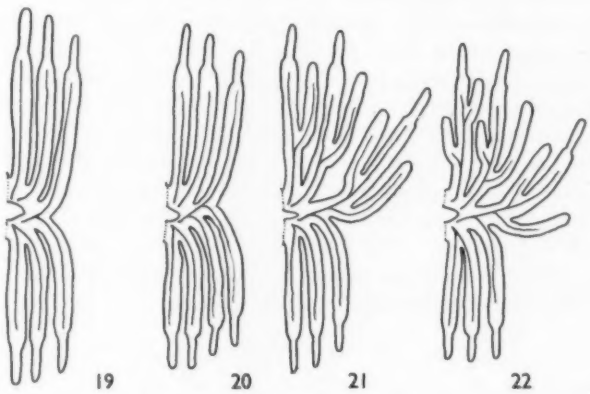
c. Anal papillae

The anal papillae are eversible tubes that can be protruded through the anal fold. In the retracted position the tubes lie in the body cavity alongside



Figs. 13–18—Chaetotaxy maps of last two segments of the third instar larvae of : (13) *Eumerus strigatus* Fall., (14) *Merodon equestris* F., (15) *Cheilosia* sp., (16) *Sericomyia lappona* L., (17) *Callicera rufa* Schumm., (18) *Syrphus balteatus* Degeer.

the hindgut and open into the perianal cavity. They are retracted by a series of muscles from the tip of each tube to the dorsal body wall. The tubes are protruded by blood pressure. Each tube has a fairly large trachea running along it. The anal papillae are bilaterally symmetrical. Typically on each side there are six papillae so arranged that three protrude anteriorly and three posteriorly (Fig. 19). The two lateral tubes (outer anterior and outer posterior) have a common base and are supplied by two branches of a single trachea. The two posterior tubes are similarly paired. In some larvae there are more than six tubes but these have resulted from further branching of the original six papillae. A formula has been devised for the number and arrangement of the papillae. The basic arrangement (Fig. 19) has the formula 1 : 1 : 2 : 2, where each number is the number of papillae with a common tracheal supply, starting from the anterior mid line. The papillae shown in Figs. 20–22 have the formulas 1 : 1 : 3 : 2, 2 : 2 : 4 : 2, 3 : 3 : 4 : 2, respectively.



Figs. 19–22—Left halves of the evaginated anal papillae of third instar larvae of : (19) *Eristalis sepulchralis* L., (20) *Myiatropa florea* L., (21) *Eristalis tenax* L., (22) *Eristalis arbustorum* L. The line inside the papillae represents the tracheal supply.

d. Spiracles

The first instar larvae are metapneustic with only the posterior spiracles functional. In most species prothoracic spiracles appear in the second instar, but in the Eristalini they only appear in the third instar. *Chrysogaster* and *Microdon* are metapneustic in all three instars.

The spiracles of the early stages are similar to those of the third instar but usually less elaborate. They may be, for example, only two slits instead of three on the posterior spiracles.

The posterior spiracles of the third instar larva are always fused together. The only exception to this is *Mesogramma*, a pollen feeding larva of the Syrphinae type, which has the posterior spiracles slightly separated in the third instar larva (Heiss, 1938). The general structure and method of moulting are typical for cylorrhaphous Diptera (Keilin, 1944). There are usually three

slits on each side and the scars are central. This is not so with the highly modified root-piercing spiracles of *Chrysogaster hirtella* (Hartley, 1958). The external structure of the posterior spiracles of some Syrphinae has been excellently shown by Bhatia (1939). In the Syrphinae the slits are usually radial and straight. The disc of the fused spiracles is rounded and the slits are on ridges. The other larvae have basically a flat disc with the slits level on the surface and arranged circumjacently. In some species with very large spiracles the slits have become subdivided into numerous radial slits (*Volucella*) or into numerous small oval openings (*Microdon*). When the spiracles are borne on a long telescopic breathing tube the disc becomes smaller and domed and the slits shorten.

The posterior spiracles of most saprophagous larvae bear four pairs of plumose setae, which are sometimes branched, on the periphery of the disc. These have articulated bases and are strongly hydrophobic.

The prothoracic spiracles, when present, are dorso-lateral near the posterior edge of the segment. They are usually small with few oval openings. In some of the larger larvae these spiracles are more elaborate and have many openings around the periphery of the spiracle. The prothoracic spiracles of the Eristalini are, however, quite different. They are large and elongated and have numerous facets each with a single opening. These spiracles also differ in that they are normally recessed in cuticular sheaths and can be protruded by a series of small protractor muscles on the sheath (Fig. 23).

The large rat-tailed larvae also have dilated tracheal trunks that can be seen through the cuticle. The shape of these is characteristic for different genera. In *Eristalis* they are straight, in *Helophilus* they undulate, and in *Sericomyia* there is a constriction in the middle.

THE PUPARIUM

The pupa is formed within the third instar larval cuticle, which is modified to form a puparium. At puparium formation the larva contracts, becomes stouter, and the head is completely withdrawn. It ceases to be mobile and the cuticle gradually becomes hardened. Later the pupal spiracles are pushed out through the puparium, through the circular patches on the dorsum of the first abdominal segment. Only the prothoracic spiracles have been functional in the amphipneustic larvae since puparium formation commenced. The prothoracic spiracles cease to be functional just before the pupal spiracles appear. Emergence of the adult is facilitated by two opercula. These are bounded by a line of thinner cuticle which becomes a line of weakness when the puparium hardens. The lines can be seen on the fully grown larva and are shown as broken lines on the chaetotaxy map (Fig. 2). One operculum consists of the dorsal part of the thoracic segments and the other of the dorsal part of the first abdominal segment.

CLASSIFICATION

The study of the larvae has shown that they form some distinct groups, and that some of these groups do not agree entirely with any of the previous classifications. Two of the present subfamilies appear to be heterogeneous.

These are the Eristalinae including *Merodon*, and the Cheilosiinae including *Ferdinandea, Pipiza, Sphegina, and Chrysogaster*. *Merodon* larvae very closely resemble *Eumerus* larvae in mouth parts, chaetotaxy, absence of prolegs, body form, and pupal spiracles ; they do not resemble Eristaline larvae in any of these features. The adults of some of the continental species also closely resemble each other (E. A. Fonseca, personal communication). *Pipiza* and related genera have aphidophagous larvae, with features as in the Syrphinae genera. *Ferdinandea, Sphegina*, and *Chrysogaster* have general saprophagous features but are themselves in distinct groups.

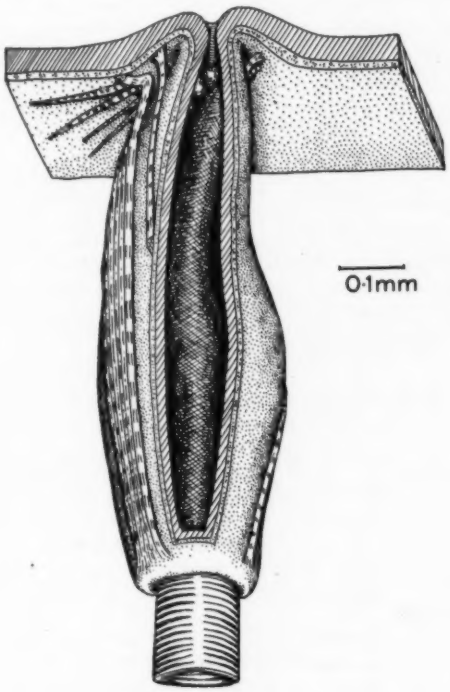


Fig. 23—*Eristalis arbustorum* L., third instar larva ; internal view of the prothoracic spiracular sheath, cut to show spiracle ; the protractor muscles are seen on the sheath.

An outline of the natural groups, as shown by the larvae, is intended in this revised classification. Only two subfamilies and several tribes are recognized. The two subfamilies have very distinct larval characters as are shown in the key. The Syrphinae have not been further studied. The tribes recognized in the Milesiinae are distinguished by the features in the key, and by the form of the pupal spiracles : long and stout—Eristalini ; long and slender—Spheginini, Chrysogastrini ; short and stout—Milesiini, Volucellini. The Spheginini also differ from the Milesiini in the form of the cephalopharyngeal skeletons. The Syrphinae are distinct from the Milesiinae in that their

pupal spiracles are very small and in most species not protruded through the puparium.

It is probable that the original syrphid larva had the following features:

1. Fused posterior spiracles on a short telescopic breathing tube.
2. Saprophagous mouth parts.
3. Prolegs on mesothorax and first six abdominal segments.

The following trends are evident:

1a. Reduction in size of the fused posterior spiracles and lengthening of the breathing tube.
1b. Loss of a telescopic breathing tube.
2a. Development of phytophagous mouth parts.
2b. Development of carnivorous mouth parts.
3. Loss of prolegs.

The development of carnivorous mouth parts is considered to have occurred only once.

The presence of the fused posterior spiracles throughout the family implies the possession of a breathing tube. This means that the larvae lived in wet situations of low oxygen tension. The possession of a breathing tube also enables the larvae to live continually near the bottom of such a medium when prolegs become advantageous (Hinton, 1955). The diversity of form amongst the Milesiini, which live in wet rot-holes of trees, suggests that this may be the ancestral group in the ancestral habitat.

Comparison of the Classification used in this work with that used by Coe (1953 *a*)

Present work	*Coe* (1953 *a*) *and Hull* (1949)
Syrphinae	Syrphinae, Chrysotoxinae, Part Cheilosiinae (*Pipiza*, *Pipizella*, etc.).
Milesiinae	
Milesiini	Xylotinae, Eumerinae, *Merodon*, Sericomyiinae, Part Cheilosiinae (*Ferdinandea*, *Brachyopa*, *Rhingia*, *Myolepta*, *Psilota*, *Hammerschmidtia*, *Cheilosia*).
Callicerini	Callicerinae.
Chrysogastrini	Part Cheilosiinae (*Chrysogaster*).
Spheginini	Part Cheilosiinae (*Sphegina*, *Neoascia*).
Eristalini	Eristalinae (except *Merodon*).
Volucellini	Volucellinae.
Microdontini	Microdontinae.
Unknown position	Pelecocerinae.

KEYS TO THE THIRD INSTAR LARVAE WITH DESCRIPTIONS OF THE LARVAE AND PUPARIA AND NOTES ON THEIR BIOLOGY

The measurements given in the following descriptions tend to be maximal and should only be taken as an approximate guide. Where there is a distinct tail the measurement of the length is given in two parts, body length and tail length; the tail is not included in the puparium measurements. The puparium

measurements are a more accurate guide to the sizes of the species. The various terms used are all explained under the appropriate section on the general morphology.

KEY TO THE TRIBES

1. With piercing mouth parts. Posterior spiracles sessile, with simple pattern on curved disc, slits more or less radial and usually straight on slight ridges (except in *Xanthogramma* where the slits are convoluted, but still distinctly radial); prothoracic spiracles very small. Prolegs vestigial or absent, without crochets; body often flattened, anterior end usually pointed; usually with colour pattern which is lost on death. Predacious mainly on aphids ..... Syrphinae.

—. Without piercing mouth parts. Posterior spiracles on a telescopic breathing tube; or if sessile, then with the slits basically more or less circumferential, usually convoluted and sometimes subdivided or as numerous small apertures, not on raised ridges; prothoracic spiracles present or absent. Prolegs with crochets present or absent. Shape varied, never with colour pattern but sometimes with brownish cuticle ..... Milesiinae....2.

2. Anterior end pointed; posterior spiracles with slits subdivided and radial; well developed prolegs with few stout crochets. (In nests of bees and wasps) ..... Volucellini (p. 565).

—. Anterior end truncate or rounded; posterior spiracles with undivided slits, or if with divided slits prolegs absent..... 3.

3. Body more or less hemispherical and flattened ventrally, pro- and mesothorax very reduced and only visible on ventral side. (Prolegs absent; pubescence usually as a lateral fringe and reticulate pattern dorsally; metapneustic)..... Microdontini (p. 568).

—. Body more or less cylindrical, pro- and mesothorax well developed, similar in size to the other segments..... 4.

4. Abdomen abruptly tapering to a long tail sheathing long telescopic breathing tube; anterior spiracles elongate (Figs. 76–88) and can be retracted into body. (The rat-tailed larvae) ..... Eristalini (p. 548).

—. Abdomen gradually tapering or truncate, if forming a distinct tail anterior spiracles squat (Fig. 25) and not retractable.... 5.

5. Metapneustic. (Small white larvae less than 10 mm.; with relatively long pubescence posteriorly, masking the lappets; posterior spiracles convex or stylet-like, on telescopic breathing tube) ..... Chrysogastrini (p. 543).

—. Amphipneustic (the anterior spiracle is often very difficult to see)..... 6.

6. Body short (less than 8 mm.) and flattened with abdomen gradually tapering posteriorly but not forming a distinct tail; prolegs and crochets present..... Spheginini (p. 538).

—. Body longer (more than 10 mm.) and more or less cylindrical, or if short and flattened posterior end truncate and without prolegs ..... 7.

7. Abdominal prolegs large and partially fused in segmental pairs, with crochets of each pair of prolegs confluent. (Single pair of long pointed lappets at end of abdomen)..... Callicerini (p. 537).

—. Prolegs separate, or absent, crochets never confluent..... Milesiini (p. 520).

KEY TO THE MILESIINI

1. Prolegs vestigial or absent, without crochets. Posterior spiracles sessile or at most only slightly retractile.....	13.
—. Prolegs present with crochets. Posterior spiracles always on longer or shorter breathing tube	2.
2. Posterior spiracles on strongly sclerotized tube at least one quarter body length ; prolegs and crochets absent on last three abdominal segments.....	*Ceriodes* (not British).
—. Posterior spiracles on strongly sclerotized tube much less than one quarter body length (although this may be on a longer but distinctly less sclerotized breathing tube) ; prolegs with crochets on first six abdominal segments.....	3.
3. Posterior end of abdomen drawn out in distinct tail sheathing a long telescopic breathing tube (at least half as long as body when extended)	4.
—. Posterior end of abdomen not forming a distinct tail although it may be long and tapering	6.
4. Tail as long as body, not appreciably wider at base ; breathing tube when extended much longer than body ; large species (20 mm.)	*Sericomyia lappona* (p. 521).
—. Tail shorter than body, noticeably wider at base ; breathing tube when extended not much longer than body ; smaller species (10–15 mm.).....	5.
5. Pubescence on anterior fold of prothorax not stouter than the rest of the pubescence. (Dorsal side of last two abdominal segments distinctly warty).....	*Myolepta luteola* (p. 522).
—. Pubescence on anterior fold of prothorax stouter than the general pubescence	*Cynorrhina*, *Calliprobola* (see under Myolepta notes page 523).
6. Posterior end of body long and tapering ; body nearly as long behind the anus as in front ; stouter spinules present only on anterior fold of prothorax ; (lappets very small and inconspicuous).....	*Pocota personata* (see Aubertin 1928).
—. Posterior end of body truncate, or if tapering, not more than one third of length behind anus ; stouter spinules present on anterior fold of prothorax and elsewhere, or with stout hooks	7.
7. Stout heavily sclerotized hooks absent.....	8.
—. Stout heavily sclerotized hooks present	11.
8. Sclerotized spinules on prothorax not appreciably taller than pubescence. (length under 12 mm.)	*Syritta pipiens* (p. 524).
—. Sclerotized spinules on prothorax distinctly taller than pubescence	9.
9. Posterior spiracles with only slightly curved slits (Fig. 32) ; hindermost lappets with about 15–20 spinules along posterior side	*Xylota sylvarum* (p. 527).
—. Posterior spiracles with strongly curved slits (Fig. 31) hindermost lappets only with about 9–12 spinules along posterior side	10.
10. Felt chamber one third length of sclerotized part of posterior spiracles ; stouter spinules on prothorax not longer than prothoracic spiracle.....	*Xylota xanthocnema* (p. 527).
—. Felt chamber more than one quarter length of sclerotized part of posterior spiracles ; stouter spinules on prothorax longer than prothoracic spiracle	*Xylota segnis* (p. 525).

11. A pair of large hooks with a common base dorso-laterally, and a single small hook laterally on the prothorax ; disc of posterior spiracles with sharp angles (Fig. 33) ..... *Xylota nemorum* (p. 529).
—. Not as above ..... 12.
12. With several large hooks and spines on pro- and mesothorax (Fig. 35) ..... *Criorhina berberina* (p. 529).
—. With hooks otherwise ..... *Brachypalpus, Tropidia**.
13. Mouth hooks absent ; lappets long or modified to spines bearing setae ..... 14.
—. Mouth hooks present ; lappets very short, or if long the middle lappet is bilobed ..... 16.
14. Pubescence fine, colourless ..... *Ferdinandea cuprea* (p. 531).
—. Pubescence coarse, or sparse and very dark ..... 15.
15. Pubescence well developed as long black spinules ..... *Rhingia campestris* (p. 534).
—. Pubescence sparse, mainly replaced by darkened blotches of cuticle (Fig. 45) ..... *Brachyopa* (p. 533).
16. Posterior spiracles shorter than broad, completely sessile ; segmental sensilla each with a single large seta ..... *Merodon equestris* (p. 536).
—. Posterior spiracles longer than broad ; sensilla each with at least two setae ..... 17.
17. Posterior pair of lappets nearly as long as the posterior spiracles; middle lappets bilobed each lobe with a conspicuous sensillum (Fig. 47) ..... *Eumerus*...18.
—. Posterior pair of lappets shorter than posterior spiracles ; middle lappets undivided (Fig. 46). (Prothoracic spiracles with a semicircle of facets) ..... *Cheilosia* (p. 536).
18. Pronounced groove between mouth hooks, mouth hook with usually seven teeth ..... *E. strigatus* (p. 535).
—. Shallow groove between mouth hooks, mouth hook usually with five teeth ..... *E. tuberculatus*.

SERICOMYIA LAPPONA Linnaeus

Third instar larva : Length, 24+24 mm. ; breadth, 6 mm. Body (Fig. 24) almost cylindrical ; thorax large ; anterior end truncate ; posterior end abruptly tapering after the anus to form a long tail sheathing a long telescopic breathing tube. Cuticle whitish, pubescence well developed, short, but sparse on dorsum of posterior end of the body ; spinules slightly stouter on anterior fold of prothorax, slightly longer on lateral ridges posteriorly ; pubescence very dense on tail. Chaetotaxy of the *Syritta* type (Fig. 9) with arrangement on tail as shown in Fig. 16 ; papillae small, setae mainly smaller than pubescence. Prolegs small ; crochets large ; abdominal prolegs with six primaries, seven secondaries, and accessories ; crochets numerous on mesothoracic prolegs. Anterior spiracles short and stout (Fig. 25), scarcely taller than wide, pale brown. Posterior spiracles very similar to those of *Eristalis*, with eight plumose terminal setae. Anal papillae long, 1 : 1 : 2 : 2, but with the three anterior papillae (1 : 1 : 1/2) densely covered with smaller, slender and pointed papillae, whereas the three posterior papillae are simple.

Puparium : Length, 11 mm. ; breadth, 6 mm. Strongly inflated, rounded anteriorly ; tapering posteriorly with dorsal surface continuing high well to

* Larvae of the North American species *Brachypalpus rileyi* Williston (Greene, 1923), *B. frontosus* Loew and *Tropidia quadrata* Say (Heiss, 1938) have hooks so it is probable that the British species do also—see also taxonomic notes after *Xylota nemorum* (p. 529).

the posterior ; pale brownish and semi-transparent ; spiracles (Fig. 36) short, stout, and curved outwards.

Taxonomic notes : The larvae of this genus are unlikely to be confused with any others except the Eristalini, from which they can best be separated by the form of the anterior spiracles, and by the tendency for the thorax to be more distended than the rest of the body.

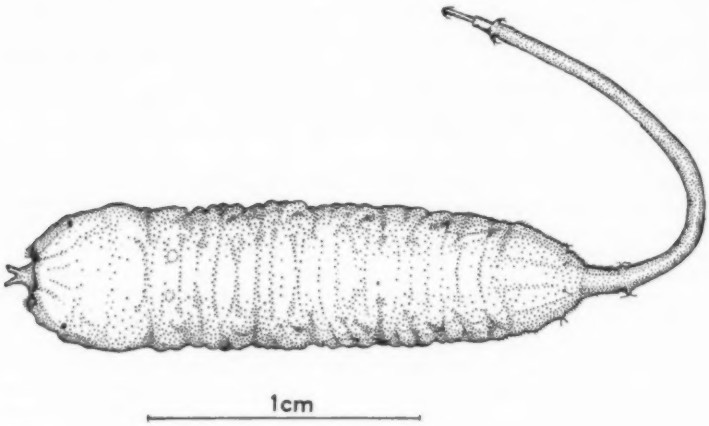


Fig. 24—*Sericomyia lappona* L., third instar larva, dorsal view.

Biological notes : This species was found in disturbed peat lying in water at the end of a cutting that had been derelict for a few years. The larvae were found in April and were already beginning to pupate in the drier peat above water level.

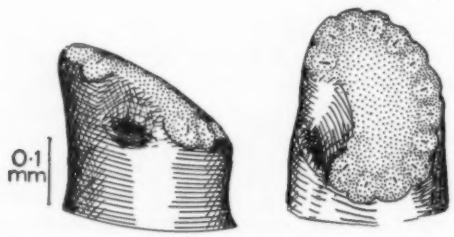


Fig. 25—*Sericomyia lappona* L., third instar larva, prothoracic spiracle.

MYOLEPTA LUTEOLA Gmelin

Third instar larva : Length, 14+4 mm. ; breadth, 3 mm. (Fig. 26). Nearly cylindrical, truncate anteriorly ; posterior end abruptly narrower and tapering, forming a short tail, sheathing long breathing tube (8 mm. extended). Cuticle mostly smooth but warty on dorsal side of last two segments, semi-transparent,

and whitish ; pubescence well developed, short and very fine ; not stouter on prothorax, sparse larger spinules on dorsal side of last two segments where the cuticle is warty instead. Chaetotaxy as *Sericomyia* (Fig. 16), with the two VLs partially fused ; papillae and setae of seventh and eighth abdominal segments prominent, elsewhere very small, posterior sensilla of eighth segment on pair of long slender lappets. Prolegs small with seven or eight primary crochets and several smaller. Anterior spiracles small, short, and slightly bilobed with two slits. Posterior spiracles small and narrow, disc (Fig. 27) small with little pattern ; slits nearly straight, short ; terminal setae with at least two branches in the anterior and posterior pairs. Anal papillae simple, 1 : 1 : 2 : 2.

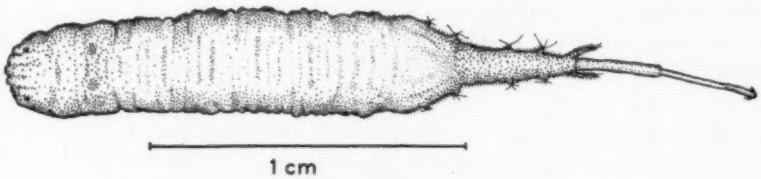


Fig. 26—*Myolepta luteola* Gmelin, third instar larva, dorsal view.

Puparium : Length, 6 mm. (plus 2 mm. for shrivelled eighth segment) ; breadth, 3 mm. Strongly inflated, anterior end abruptly rounded, posterior end rounded ; greyish brown but covered with chalky excretion at time of puparium formation ; spiracles (Fig. 41) reddish brown.

Taxonomic notes : This species resembles at first glance one of the " rat-tailed " maggots of the Eristalini from which it differs in several ways ; anterior spiracles ; posterior spiracles ; the differently shaped and much shorter tail ; and the arrangement of the associated sensilla ; also the pupal spiracles. The larva of *Calliprobola speciosa* Rossi figured and described by Girschner (1884) is also of this type. It would appear to differ from *Myolepta* by possessing a longer and more slender tail, which also has a pair of elongate tapering lappets at its end. Other rather similar larvae with stouter prothoracic spinules are those described by Greene (1917, 1923) as *Criorhina* species.*

Biological notes : The larvae were found in a small rot-hole of an old beech (*Fagus sylvatica*) from which was dripping a black watery liquid, at about ten feet above ground level in May, and they pupated soon afterwards. The larvae have also been found in poplar (*Populus* sp.) according to Becher (1882). It is interesting to note that while these larvae live in tree rot-holes, they have none of the rasping structures possessed by other larvae living in similar habitats.

* The North American species described by Greene : *Criorhina* (*Somula*) *decora* Macquart, *Criorhina pictipes* Bigot, and *Blera* (*Criorhina*) *umbratilis* Williston ; are probably not *Criorhina* Meigen (*Penthesilea* Meigen) but *Cynorrhina* Williston (*Blera* Billberg) of which *Somula* Macquart is regarded by Hull (1949) as a subgenus with *decora* Macquart as the genotype.

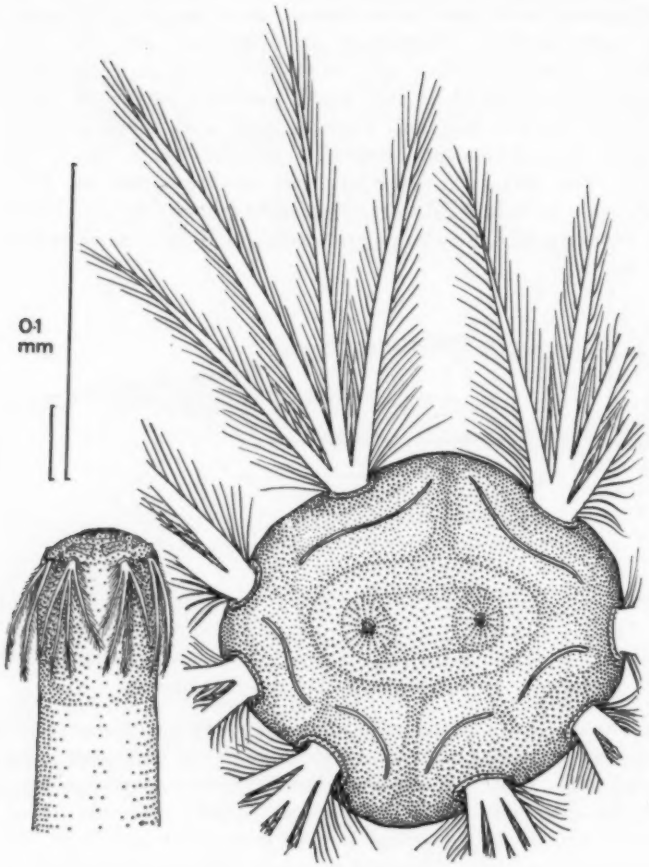


Fig. 27—*Myolepta luteola* Gmelin, third instar larva, posterior spiracles.

SYRITTA PIPIENS Linnaeus

Third instar larva : Length, 12 mm. ; breadth, 3 mm. Almost cylindrical, slightly flattened below, widest about the middle ; anterior end truncate, prothorax slightly less deep than at the middle ; posterior end only slightly tapering to end ; three pairs of lappets on the eighth abdominal segment ; no breathing tube but posterior spiracles can be partially retracted. Cuticle yellowish white ; pubescence well developed, fine and short ; spinules on anterior prothorax stouter and lightly sclerotized ; three groups of stouter sclerotized spinules either side laterally on the prothorax arranged as follows : (*a*) a group of 4 or 5 just posterior to PL2, (*b*) another group of 4 or 5 behind (*a*), just anterior to MSL1, and (*c*) a group of 6 below (*b*) and anterior to MSL3 : the positions of these are shown on the chaetotaxy plan. Chaetotaxy as shown

(Fig. 9), papillae and setae small ; two sensilla on the first lappet, one on the second, and two on the third. Prolegs small, on mesothorax and first six abdominal segments ; crochets small but well formed ; abdominal prolegs with five or six primaries, four or five secondaries, and some tertiaries ; some crochets on the sixth abdominal prolegs anteriorly directed ; mesothoracic prolegs with about eight primaries ; there are a few small crochets on the metathorax in the homologous position as those on the mesothoracic prolegs. Anterior spiracles very small, similar in appearance to those of *Sphegina* (Fig. 51). Posterior spiracles 0·8 mm. long, three times as long as broad ; disc as shown (Fig. 29), terminal setae much branched, as long as width of disc. Anal papillae simple, formula 1 : 1 : 2 : 2.

Puparium : Length, 6 mm. ; breadth, 3 mm. Strongly inflated ; rounded anteriorly and tapering posteriorly, with dorsal surface parallel to ventral surface up to seventh abdominal segment where it abruptly descends to a shrunken eighth segment ; brownish yellow and semi-transparent ; spiracles short, with distal half swollen (Fig. 42).

Taxonomic notes : Very similar to the *Xylota segnis* group, but smaller and with weaker pubescence ; the disc of the posterior spiracles is quite distinct.

Biological notes : The larvae have been found in various sorts of decaying matter such as manure heaps and the edge of silage clamps. They have been found in vast numbers in the latter situation. The larvae overwinter and emergence starts in March, there is probably a second generation during the summer.

XYLOTA SEGNIS Linnaeus

Third instar larva : Length, 15 mm. ; breadth, 4 mm. (Fig. 28). Shape as *Syritta pipiens*, but eighth abdominal segment rather more elongate with very short breathing tube bearing the fused posterior spiracles. Pubescence well

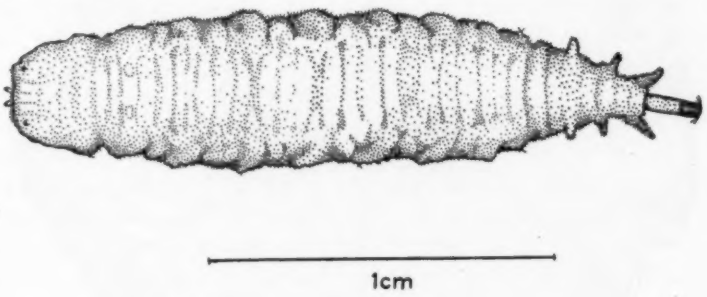
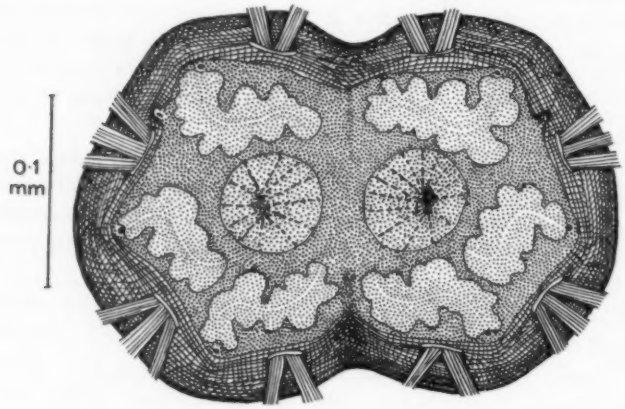


Fig. 28—*Xylota segnis* L., third instar larva, dorsal view.

developed ; spinules on anterior fold and in lateral patches stouter and well sclerotized, as tall as the prothoracic spiracles ; arrangement of these spinules as *S. pipiens* except that the anterior group (*a*) extend dorsally to form an irregular band some two spinules length behind the anterior prothoracic group,

and behind PD1 and PD4. Chaetotaxy as *Syritta pipiens*. Prolegs moderate, crochets large ; abdominal prolegs with five to six primaries, and as many secondaries, and numerous accessories ; mesothoracic prolegs with more crochets ; several crochets as large as the secondaries present on the metathorax in the homologous position of the mesothoracic prolegs. Anterior



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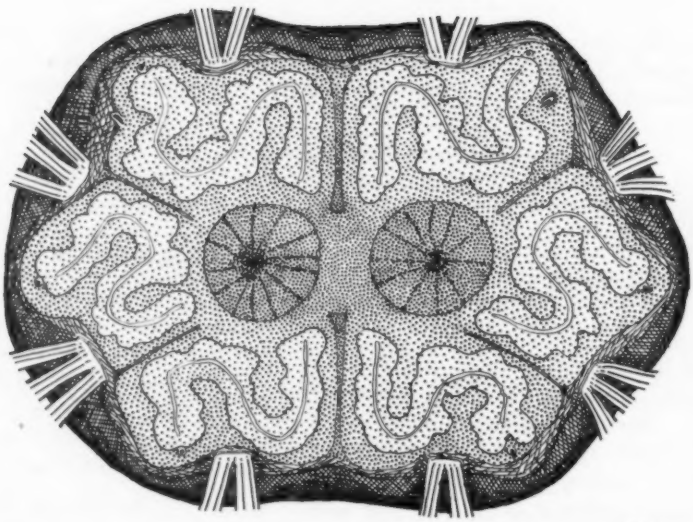

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Figs. 29–30—Discs of posterior spiracles of third instar larvae of : (29) *Syritta pipiens* L., (30) *Xylota segnis* L.

spiracles small with four slits. Posterior spiracles 1·4 mm. long, three times as long as broad, felt chamber 1/4 length of spiracles ; disc as shown (Fig. 30) ; terminal setae much branched each as large as disc. Anal papillae simple : 1 : 1 : 2 : 2.

Puparium : Length, 9 mm. ; breadth, 4 mm. Shape similar to *Syritta pipiens* but more elongate and not so inflated, brownish ; spiracles relatively long (Fig. 37) curved forward and outward.

Taxonomic notes : The *Xylota segnis* group and *Syritta pipiens* show many features in common and are thus difficult to separate ; *X. sylvarum* has a distinct posterior spiracular disc and is the largest species, it also has pupal spiracles with fine spine-like projections—a feature also found in *X. xanthocnema* but not in *X. segnis*. *X. segnis* is smaller than *xanthocnema* but has bolder stout spinules ; the posterior spiracles of *xanthocnema* are parallel sided, and more slender than those of *segnis* which are distinctly wider at the base.

Biological notes : X. segnis appears to have fairly wide food habits and has been found in the following situations : very wet decomposing silage, wet sawdust of an old saw pit, exudate and rot-holes of yew (*Taxus baccata*), and wet decaying beech stumps (*Fagus sylvatica*). *X. sylvarum* has been found in wet sawdust and under the decomposing bark of a beech stump on the bank of a stream ; *X. xanthocnema* has only been found in the exudate and rot-holes of yews.

The larvae overwinter and pupation starts in the spring, it is doubtful whether a second generation ever occurs during the summer. Some larvae of *X. xanthocnema* have been found in the early spring that have required another year to complete their development.

XYLOTA SYLVARUM Linnaeus

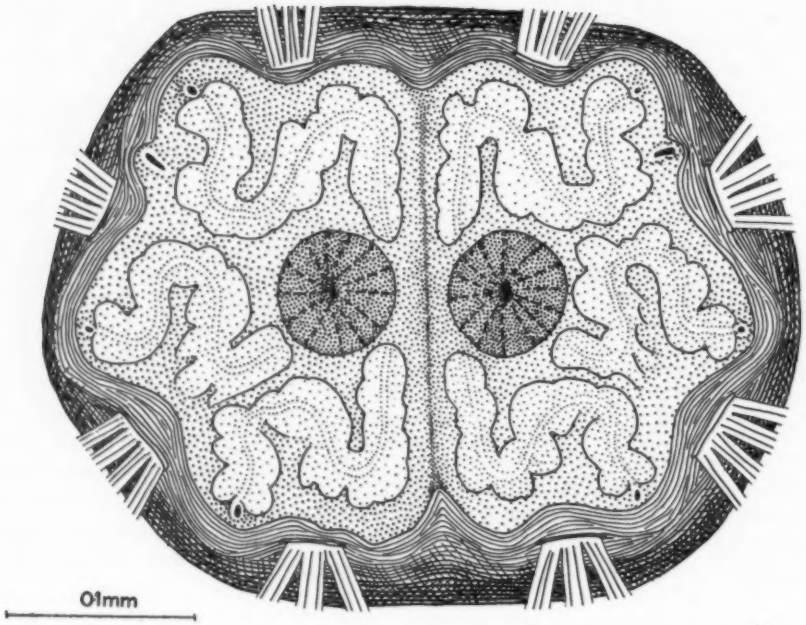
Third instar larva : Length, 20 mm. ; breadth, 4·5 mm. Shape similar to *X. segnis* with posterior end even more elongate so that one-third body length is after the anus ; the pairs of lappets separated by distance at least as long as the lappets in an extended larva ; breathing tube as long as posterior spiracles. Pubescence well developed ; sclerotized prothoracic spinules arranged as *segnis* but with dorsal group sparse, short compared with prothoracic spiracle. Posterior spiracle 2 mm. long, five times as long as broad ; slit pattern on disc simple (Fig. 32). Other features as *segnis*.

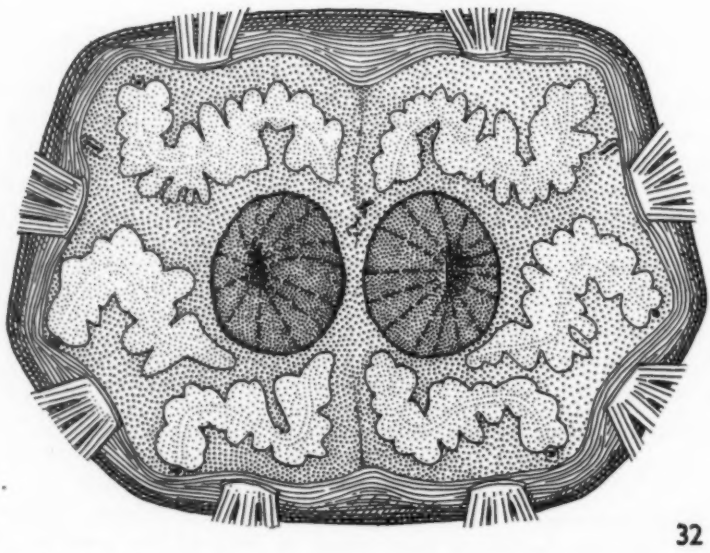
Puparium : Length, 12 mm. ; breadth, 5 mm. Shape as *S. pipiens*, brownish ; spiracles (Fig. 39) short with fine cuticular projections radially from the spiracular openings, yellowish brown.

Notes : See *X. segnis*.

XYLOTA XANTHOCNEMA Collin

Third instar larva : Length, 16 mm. ; breadth, 3·5 mm. Shape as *X. segnis*, but with breathing tube nearly as long as the posterior spiracles. Pubescence well developed ; sclerotized prothoracic spinules smaller than prothoracic spiracles, arrangement as *segnis* except that the dorsal band is





Figs. 31–32—Discs of posterior spiracles of third instar larvae of: (31) *Xylota xanthocnema* Collin, (32) *Xylota sylvarum* L.

reduced to a few scattered spinules. Posterior spiracle 1·2 mm. long, three and a half times as long as broad, disc (Fig. 31) very similar to *segnis*. Other features as *segnis*.

Puparium : Length, 9 mm. ; breadth, 4 mm. Shape as *S. pipiens*, brownish ; spiracles (Fig. 38) short with fine cuticular projections radiating from the openings, yellowish brown.

Notes : See *X. segnis*.

XYLOTA NEMORUM Fabricus

Third instar larva : Length, 13 mm. ; breadth, 3 mm. Shape as *Syritta pipiens* with short breathing tube. Pubescence well developed ; stouter spinules limited to anterior fold of the prothorax ; two large heavily sclerotized hooks with a common base either side antero-lateral to the prothoracic spiracles in the (*b*) position (see *Syritta pipiens*) and a single smaller well sclerotized hook below these in the (*c*) position. Chaetotaxy as *S. pipiens*. Crochets large ; six primaries, secondaries and tertiaries present ; few small crochets on metathorax, generally similar to *X. segnis*. Anterior spiracles small with four slits. Posterior spiracles 1 mm. long, three and a half times as long as broad ; distal half of spiracles with tuberculate sculpturing, basal half smooth ; disc (Fig. 33) angular ; terminal setae branched, each as large as disc. Anal papillae simple : 1 : 1 : 2 : 2.

Puparium : Length, 7 mm. ; breadth, 3 mm. Shape as *S. pipiens*, brownish ; spiracles (Fig. 43) short and curved back, yellow brown.

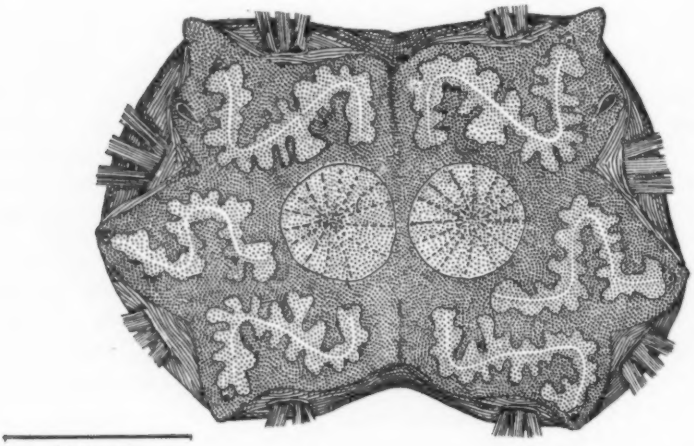
Taxonomic notes : The *Xylota nemorum* group is characterized by the presence of two pairs of very stout hooks on the prothorax as is exemplified by the North American species described by Heiss (1938) (*X. pigra*, *bicolor*, and *fraudulosa*). It is probable that the other two British species *X. abiens* Mg. and *X. florum* Fabr. are in this group. Other species known to possess large hooks on the prothorax are the North American species of *Brachypalpus* described by Greene (1923) and Heiss (1938). There does not seem to be any reliable generic feature for separating these from *Xylota nemorum* and related species. Heiss separates the species on the character of the hooks but this is liable to greater individual variation than the specific variation given. A feature that may help is that the three lappets of *X. nemorum* are approximately equal whereas in *Brachypalpus* the lappets appear to be shorter anteriorly.

Biological notes : The larvae have been found overwintering under the bark of logs and branches lying in wet situations. The larvae seem restricted to fairly recently fallen logs before much decay has set in.

CRIORHINA BERBERINA Fabricus

Third instar larva : (This description is based on the puparium only.) Length, 18 mm. ; breadth, 4 mm. Shape similar to *Syritta pipiens* with short breathing tube. Pubescence well developed, stouter spinules generally on prothorax and very stout hooks on dorsum of pro- and mesothorax as shown in Fig. 35. Chaetotaxy of the *Syritta* type. Crochets large ; five primaries, up

to eight secondaries and numerous accessories extending inwards ; rather more on the mesothoracic prolegs, and numerous large metathoracic crochets. Posterior spiracles long as broad ; disc (Fig. 34) with simple slits ; terminal setae much branched, large.



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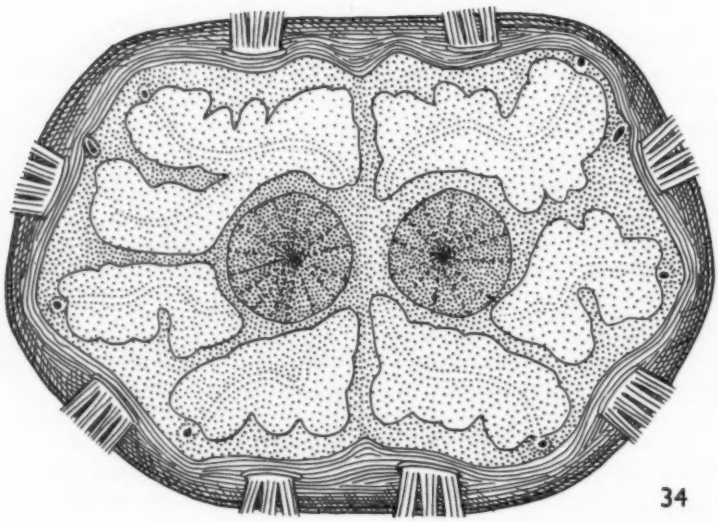

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Figs. 33–34—Discs of posterior spiracles of third instar larvae of : (33) *Xylota nemorum* F. (34) *Criorhina berberina* F., with abnormal development of a fourth slit on the left side.

Puparium : Length, 12 mm. ; breadth, 5·5 mm. Shape similar to *S. pipiens ;* spiracles (Fig. 40) stumpy, yellow-brown.

Taxonomic notes : The strong spines on the prothorax distinguish this species from others of the *Xylota* type described here, it is not known however whether the other *Criorhina* have them. See also footnote after *Myolepta*, p. 523.

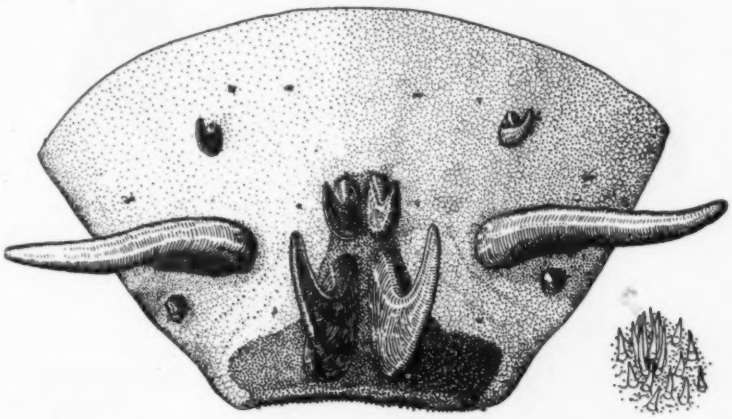


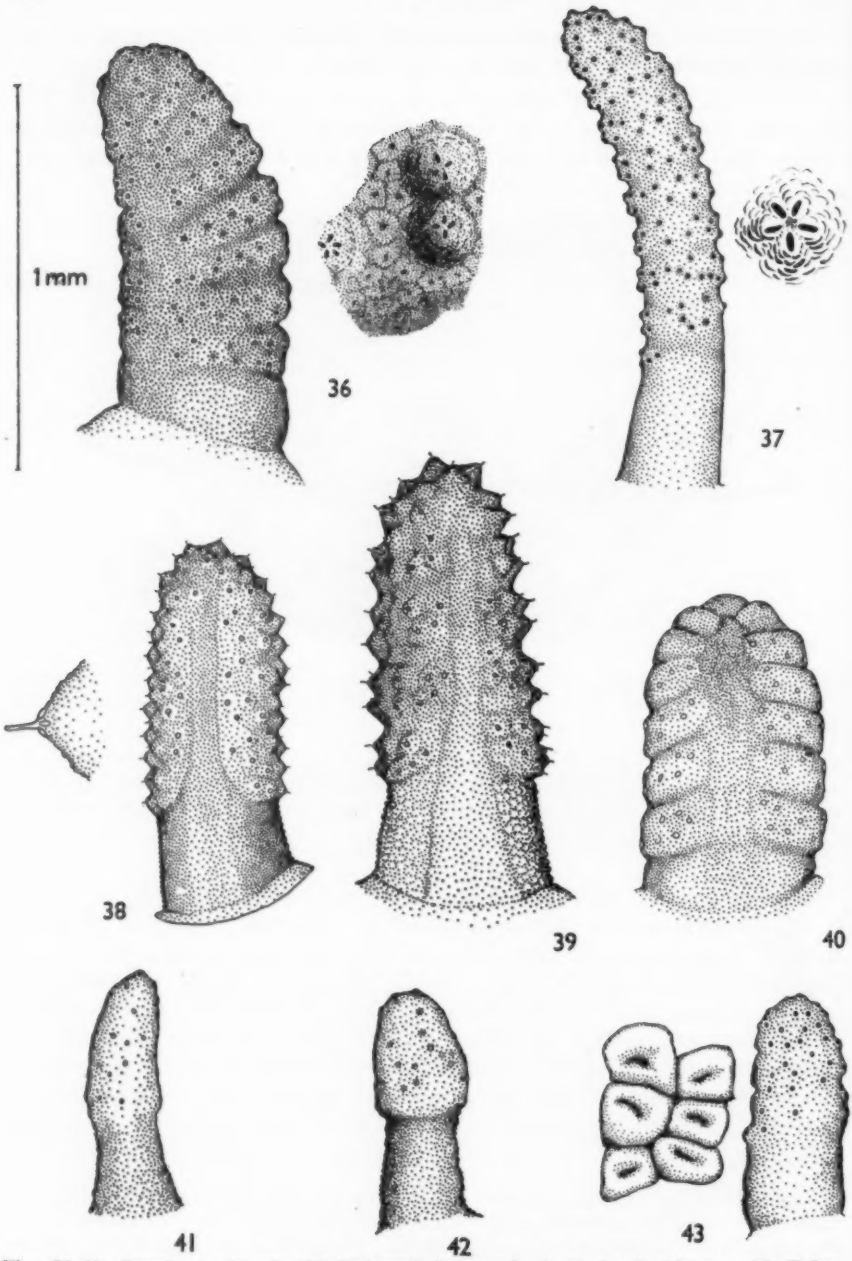
Fig. 35—*Criorhina berberina* F., third instar larva ; dorsal part of pro- and mesothorax showing hooks, inset, detail of pubescence with a sensillum (drawn from the anterior operculum of the puparium).

Biological notes : The puparium of this species was found at the base of a fallen birch (*Betula* sp.) which was found to have a slimy decay in the base of the trunk. The puparium was found in April.

FERDINANDEA CUPREA Scopoli

Third instar larva (description based on puparium) : Length, 12 mm. ; breadth, 3 mm. Almost cylindrical, slightly flattened ventrally, tapering slightly towards truncate ends ; eighth abdominal segment particularly truncate bearing three pairs of slender lappets of which the first and second are on the same vertical fold, the third is on the next fold posteriorly ; no development of a telescopic breathing tube. Cuticle whitish ; pubescence well developed, no particular differentiation of spinules even on the prothorax. Chaetotaxy as *Rhingia campestris*, papillae short and insignificant. Prolegs vestigial without crochets.* Anterior spiracles very small with two slits.

* Lundbeck (1916) describes this larva with " . . . seven pairs of slight prolegs with small spines on the first seven abdominal segments ; also on metathorax a pair are traceable ; . . ." which appears to disagree with the above description. It should be pointed out that he does not specify that the spines differ from the pubescence, and that he states these slight prolegs are present on the first seven abdominal segments as well as the metathorax, no Syrphid larvae have proper prolegs on the seventh abdominal segment although in some a slight hump is present, similarly on the metathorax.



Figs. 36–43—Pupal spiracles of : (36) *Sericomyia lappona* L., inset, detail of facets ; (37) *Xylota segnis* L., inset, detail of facet ; (38) *Xylota xanthocnema* Collin, inset, detail of facet with spine ; (39) *Xylota sylvarum* L. ; (40) *Criorhina berberina* F. ; (41) *Myolepta luteola* Gmelin ; (42) *Syritta pipiens* L. ; (43) *Xylota nemorum* F., inset, detail of basal cuticle.

Posterior spiracles 0·8 mm. long, nearly as wide as long ; somewhat conical with a distinct constriction half way along and another constriction between the two spiracles on the disc ; disc (Fig. 44) with slightly convoluted slits ; terminal setae much branched, short.

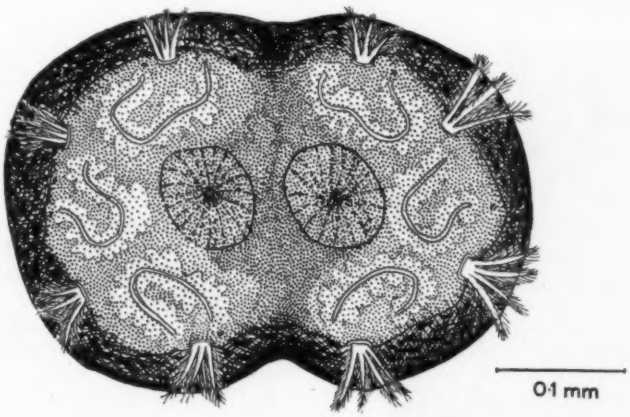


Fig. 44—*Ferdinandea cuprea* Scop., third instar larva, disc of posterior spiracles.

Puparium : Length, 8 mm. ; breadth, 3 mm. Generally rounded, inflated about the middle and tapering off towards the ends ; posterior spiracles slightly dorsal, surrounded by the lappets ; brownish yellow (pupal spiracles lost in this specimen).

Taxonomic notes : The larva is most likely, on account of its habitat, to be mistaken for one of the *Xylota* type but can easily be distinguished by the absence of prolegs and the more dorsal position of the posterior spiracles. The larva is also very similar to the *Cheilosia* type which differ principally by the possession of mouth hooks.

Biological notes : The larvae have been found in exuding wounds of trees, particularly where there has been damage by *Cossus*. The larvae overwinter and pupate in the spring.

BRACHYOPA sp.

Third instar larva : Length, 8 mm. ; breadth, 2·5 mm. Flattened dorso-ventrally ; anterior end bluntly rounded, posterior end tapering to short terminal telescopic breathing tube bearing posterior spiracles ; narrow lappets on eighth abdominal segment (Fig. 45). Cuticle greyish white, covered with dark brown blotches ; pubescence sparse ; spinules stout and dark, greatest development on anterior fold of prothorax. Chaetotaxy as shown in Fig. 10 ; papillae mainly short, setae long, often darkened. Prolegs and crochets absent. Anterior spiracles very small with two slits. Posterior spiracles 1·2 mm. long and slender ; disc domed with simple slits, no terminal setae. Anal papillae simple and very short, 1 : 1 : 2 : 2.

Taxonomic notes : The genus is very distinct, but none of the larvae has been reared successfully so that the specific differences are not known.

Biological notes : The larvae live in the exudates of various trees, especially *Ulmus* species, and are overwintering.

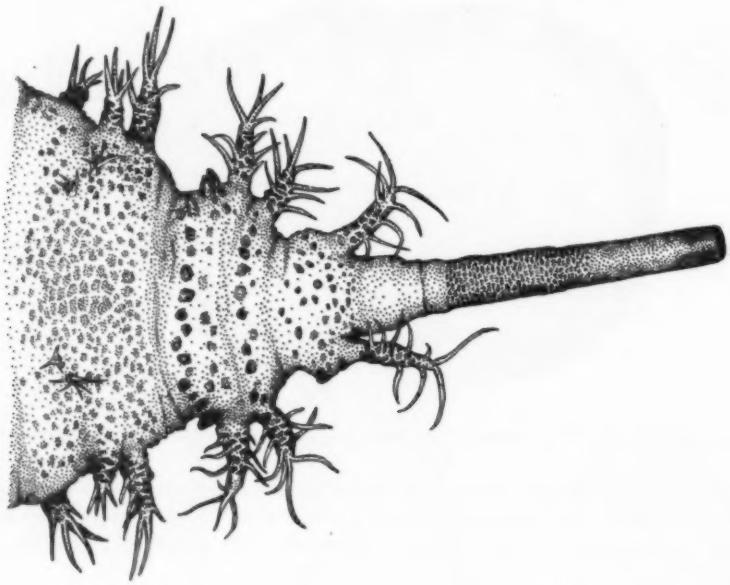


Fig. 45—*Brachyopa* sp., third instar larva, dorsal view of posterior end.

RHINGIA CAMPESTRIS Meigen

Third instar larva:* Length, 12 mm. ; breadth, 3·5 mm. More or less cylindrical ; tapering slightly towards truncate ends ; no telescopic breathing tube ; posterior spiracles slightly dorsal. Cuticle colourless and very transparent ; pubescence well developed ; spinules long and dark, not appreciably stouter on anterior prothorax. Chaetotaxy as shown (Fig. 11) ; papillae very distinct, long and thin especially posteriorly with few large dark spinules along their length, sensillum at end surrounded by numerous setae radiating outwards so that they are parallel to the surface of the body ; the posterior three pairs, which form the lappets of some larvae, are also of this spine-like form. Prolegs vestigial, no crochets. Anterior spiracles very small with two slits. Posterior spiracles 1 mm. long, one and a half times as long as wide ; conical with a constriction half way along its length, also a longitudinal constriction between the two spiracles at the disc ; terminal setae much branched, short. Anal papillae vestigial.

* A fuller account, not entirely in agreement with the following is given by Coe (1942), and another by Krüger (1926).

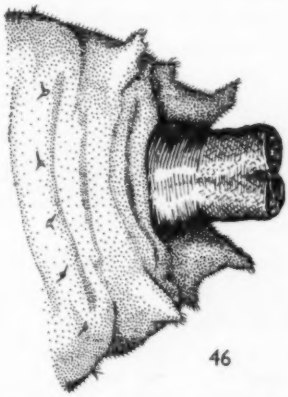
Puparium : Length, 8 mm. ; breadth, 3·5 mm. Generally rounded, inflated about the middle and tapering slightly towards the ends ; brownish and usually heavily tangled with dirt ; spiracles 0·5 mm. long ; dark brownish, stout and tapering towards end.

Taxonomic notes : The form of the pubescence and segmental papillae make this larva quite distinct from other genera.

Biological notes : The larvae live in cow dung and there are two generations a year. Eggs are laid in batches on leaves overhanging the cowpat in May–June and again in August–September, the larvae of the second brood overwinter in the soil beneath the droppings and pupate in the spring.

EUMERUS STRIGATUS Fallen.

Third instar larva : Length, 11 mm. ; breadth, 3 mm. More or less cylindrical ; very slightly tapering towards rounded ends ; three pairs of small lappets on eighth abdominal segment (Fig. 47), the second pair bearing two



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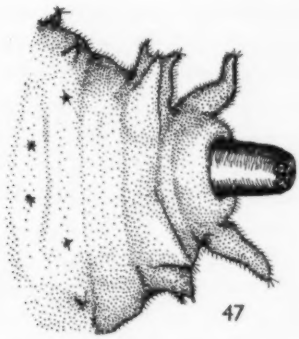

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Figs. 46–47—Dorsal views of the posterior ends of third instar larvae of : (46) *Cheilosia* sp., (47) *Eumerus strigatus* Fall.

sensilla. Cuticle whitish ; pubescence well developed, short. Chaetotaxy as shown (Fig. 13) very similar to *Merodon* (q.v.), but with two or three short setae. Dorsal mouth hooks present ; antenna complex short ; lateral lobes at sides of mouth reduced, ventral pocket beneath mouth absent. Prolegs vestigial, without crochets. Anterior spiracles small, pale brown, two openings. Posterior spiracles pale brown, 0·7 mm. long, twice as long as broad ; tapering toward disc ; disc flat, slits moderately long and curved.

Puparium (not seen) : Length, 7 mm. ; breadth, 3 mm. Anterior end rounded, posterior end slightly tapering, grey brown ; spiracles short conical, brown.

Taxonomic notes : Distinguishable from other genera by the form of the lappets, mouth hooks, and absence of prolegs. The species *strigatus* and *tuberculatus* are apparently very difficult to separate as far as is known (Hodson, 1932 a) *tuberculatus* having more slender features.

Biological notes : See Hodson (1926). The larvae are phytophagous and live gregariously in bulbs. There is one generation a year and they overwinter as larvae.

MERODON EQUESTRIS Fabricus

Third instar larva : Length, 20 mm. ; breadth, 6 mm. Almost cylindrical, widest about the sixth abdominal segment ; posterior end rounded ; very slightly tapering anteriorly to blunt anterior end ; only posterior pair of very small lappets present. Cuticle whitish ; pubescence well developed, short. Chaetotaxy of reduced form, single VL and only two V on all segments (Fig. 14) ; setae single, long and conspicuous, except D2+3 which sometimes has a smaller seta as well. Large mouth hooks present. Antenno-maxillary complex short and stout ; ventral pocket beneath the mouth absent, lobes at side of mouth very reduced. Prolegs vestigial without crochets. Anterior spiracles short and fairly stout, brown, with two long slits on end, scar half way up on outer side. Posterior spiracles dark brown, very short and massive; sessile, in slightly dorsal position ; disc flat, with long convoluted slits, terminal setae branched but very short. Anal papillae said to be absent (Heiss, 1938).

Puparium (not seen): Length, 14 mm. ; breadth, 7 mm. Strongly inflated, ends rounded ; pupal spiracles short, horn-like, dark.

Taxonomic notes : The mature larva is not likely to be confused with any other on account of its size. The very small lappets distinguish it from *Eumerus* species, which have larger lappets, and from *Xanthogramma*, which has a narrower anterior end and no lappets.

Biological notes : The biology of this species has been considered by many authors, the accounts of Hodson (1932 b)* and Doucette *et al.* (1942) being the more important. The larvae are phytophagous in various bulbs, particularly *Narcissus*, giving rise to the common name of the Narcissus Bulb Fly. There is only one generation a year, eggs are laid early in the summer on leaves of the host near the ground and hatch about ten days later, the larvae are full grown by the following spring when they pupate in the soil near the host, the adult emerges after three or four weeks. It is noticeable that this species spends a far longer time as egg and in puparium than most other Syrphidae.

CHEILOSIA Meigen

Features of some third instar larvae : More or less cylindrical ; slightly tapering anteriorly, bluntly rounded posteriorly ; three pairs of short lappets, the middle pair often vestigial (Fig. 46). Cuticle whitish, pubescence well developed, not particularly modified anywhere. Chaetotaxy reduced, only one VL (Fig. 15), two or three setae. Large mouth hooks present, lateral lobes either side of mouth reduced, no ventral pocket beneath mouth. Prolegs vestigial or absent, no crochets. Anterior spiracles short ; several slits arranged in a crescent, not unlike those of *Sericomyia lappona* (Fig. 25). Posterior spiracles sessile, length breadth ratio variable ; disc flat (in one

* Hodson states erroneously that there are four larval instars.

species at least there is a cuticular projection on the disc between the two spiracles) with long convoluted slits, that are subdivided.

Puparium : Generally inflated ; spiracles pale, more or less conical.

Taxonomic notes : The larvae can be distinguished from others with mouth hooks (*Merodon* and *Eumerus*) by the different arrangement of the sensilla on the lappets.

CALLICERINI

Larva of only one species available.

CALLICERA RUFA Schummel

Third instar larva : Length, 23 mm. ; breadth, 4 mm. Almost cylindrical, thoracic region inflated ; abruptly rounded anteriorly ; tapering from seventh abdominal segment posteriorly to short breathing tube ; one pair of conspicuous pointed slightly ventral lappets at end of eighth abdominal segment just before the breathing tube. Larva greyish white, cuticle semi-transparent ; pubescence well developed short, slightly stouter spinules on anterior fold of prothorax ; three large, curved, well sclerotized, spines on a common base either side on prothorax just below the prothoracic spiracles. Chaetotaxy of normal Milesiini form (Fig. 9), posterior end as Fig. 17, setae long and slender. Prolegs large, those of the abdomen fused ; many crochets in four or five rows which are almost confluent, on the last two pairs of prolegs

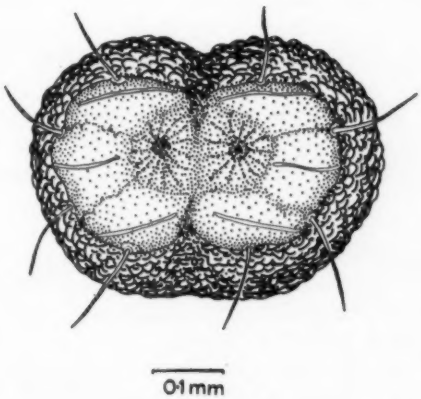


Fig. 48—*Callicera rufa* Schumm., third instar larva, disc of posterior spiracles.

the crochets are mainly anteriorly directed. Anterior spiracles small with three openings. Posterior spiracles 0·5 mm. long and almost as broad ; disc as shown in Fig. 48, slits atypical, all running transversely and straight, four pairs of simple terminal setae ; the spiracles have a rounded appearance, and are generally quite unlike those of any other semi-aquatic larvae, and more like the predatory larvae. Anal papillae long, formula 1 : 1 : 2 : 2.

Taxonomic notes : This species can be distinguished from those of other genera by the fused prolegs, the single pair of lappets, and the abnormal posterior spiracles.

Biological notes : Coe (1938) gives an account of the biology of this species as well as a description of the larva. The larvae were found living in a wet decayed cavity in the fork of a pine. Some of these larvae took five years to complete their development (Coe, 1941).

KEY TO THE SPHEGININI

1. A pair of strong hooks dorsally on the prothorax ; without groups of small hooked spines on the sides of the prothorax ; sensilla on inconspicuous papillae..... (Not enough is known about the species in this genus to enable a key to be constructed.)	*Neoascia* (p. 541).
—. Without a pair of strong hooks dorsally on the prothorax ; groups of small hooked spines on the sides of the prothorax ; lateral abdominal sensilla on prominent conical protuberances	*Sphegina*....2.
2. Abdominal sensilla on long more or less cylindrical papillae, posterior group of sensilla on particularly long papillae with pubescence extending along them (Fig. 54).....	*kimakowiczi* (p. 540).
—. Abdominal sensilla on more or less conical papillae, posterior group not on long papillae and without pubescence (Fig. 53)..	3.
3. Papillae of abdominal sensilla stoutly conical, setae stout, pubescence on eighth abdominal segment well developed (Fig. 52).....	*clunipes* (p. 538).
Papillae of abdominal sensilla slender, setae slender ; pubescence on eight abdominal segment sparse (Fig. 53).....	*verecunda* (p. 540).

SPHEGINA CLUNIPES Fallen

Third instar larva : Length, 7 mm. ; breadth, 1·5 mm. Body (Fig. 49) flattened ; tapering gradually from middle posteriorly to a short telescopic breathing tube ; anterior end truncate ; prolegs only slightly developed. Cuticle yellowish white ; pubescence colourless, short and fine; stout,

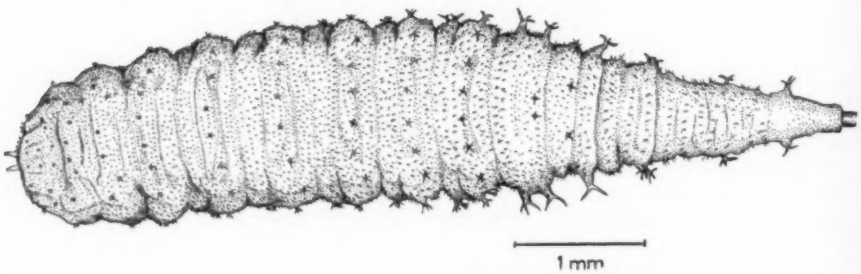
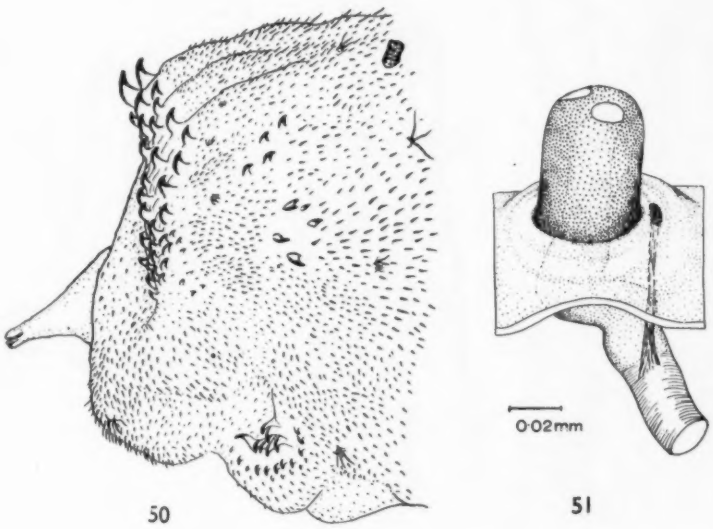


Fig. 49—*Sphegina clunipes* Fall., third instar larva, dorsal view.

moderately sclerotized, curved spines on anterior fold and in two lateral patches on side of prothorax between the lateral sensilla and the spiracle (Fig. 50) ; two rows of small straight spinules just anterior to the anus and posterior to

the A7V sensilla. Chaetotaxy as shown (Fig. 5) ; sensilla of different forms ; short setae in rosettes not on papillae ; long setae on conspicuous papillae ; and some more or less fused pairs (Fig. 1) ; sensilla larger on abdomen and especially prominent with distinctly conical papillae laterally. Prolegs poorly developed ; crochets small and lightly sclerotized, usually five primaries and some small secondaries. Anterior spiracles very small, with two oval openings (Fig. 51). Posterior spiracles of the Eristaline type, pale brown ; terminal setae paired, plumose. Anal papillae simple, formula 1 : 1 : 2 : 2.



Figs. 50–51—*Sphegina clunipes* Fall., third instar larva : (50) lateral view of anterior end, (51) prothoracic spiracle.

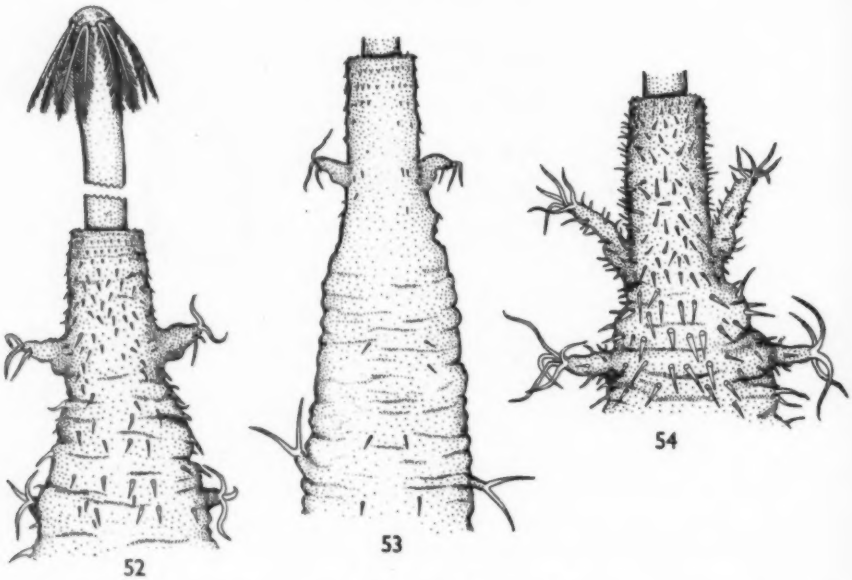
Puparium : Length, 6 mm. ; breadth, 2 mm. Anterior half strongly inflated, posterior three segments shrunken and usually curved. Cuticle semi-transparent, brownish, pubescence not darkened. Spiracles pale brownish (Fig. 55), 1 mm. long, slightly curved with distinct indentation near the tip ; facets prominent, separate, three to five openings in each facet ; length breadth ratio of spiracle 7·5 : 1.

Taxonomic notes : The larvae of this genus are very similar as are the adults. The features given in the key are the only ones available and seem to be fairly reliable. *S. clunipes* is by far the most common.

Biological notes : The larvae of all three species have been found under wet decaying bark. *S. clunipes* has also been found in the wet exudate of elms (*Ulmus*) along with *Brachyopa* larvae. There is one generation a year and the larvae overwinter.

SPHEGINA KIMAKOWICZI Strobl

Third instar larva : Length, 6 mm. ; breadth, 1·5 mm. Shape as *S. clunipes.* Pubescence colourless, short and fine ; dense and longer posteriorly, extending up papillae of posterior sensilla ; stout, moderately sclerotized, curved spines on anterior prothorax and in two lateral patches on sides of prothorax between the lateral sensilla and the spiracle. Chaetotaxy as *S. clunipes.* Papillae bearing sensilla on abdomen long and slender, almost cylindrical. Other features as *S. clunipes.*



Figs. 52–54—Dorsal views of the posterior ends of the third instar larvae of : (52) *Sphegina clunipes* Fall., (53) *Sphegina verecunda* Collin, (54) *Sphegina kimakowiczi* Strobl.

Puparium : Length, 5 mm. ; breadth, 2 mm. Shape as *S. clunipes.* Spiracles (Fig. 57) colourless, 1·1 mm. long, almost straight, without indentation near tip ; facets on slightly raised tubercles ; whole spiracle densely covered with small but prominent tubercles giving the spiracle a glistening appearance. Length breadth ratio 10 : 1.

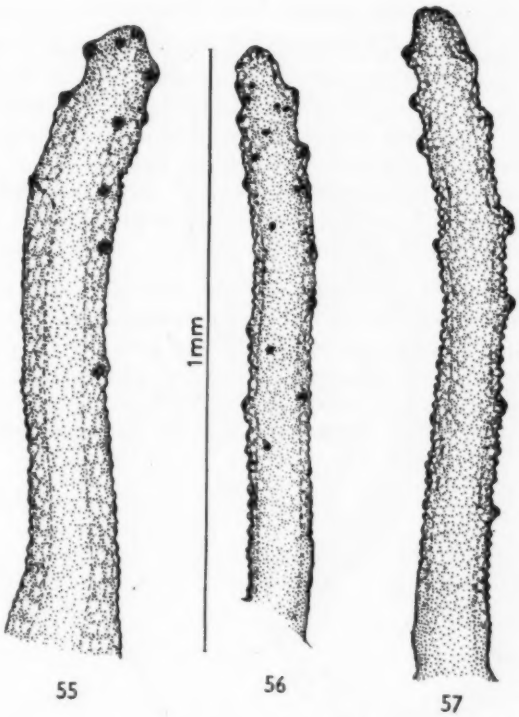
Notes : See *S. clunipes.*

SPHEGINA VERECUNDA Collin

Third instar larva : Length, 6 mm. ; breadth, 1·25 mm. Shape as *S. clunipes.* Cuticle unpigmented ; pubescence colourless, short and fine ; fairly sparse but very sparse posteriorly ; fairly stout, lightly sclerotized, curved spines on anterior prothorax and in two lateral patches on sides of prothorax between sensilla and spiracle. Chaetotaxy as *S. clunipes.* Papillae bearing sensilla small and conical, bearing few setae. Other features as *S. clunipes.*

Puparium : Length, 5 mm. ; breadth, 1·75 mm. Shape as *S. clunipes.* Spiracles (Fig. 56) brownish, 0·8 mm., long, straight, tip constricted ; facets prominent ; spiracle noticeably tuberculate. Length breadth ratio 9 : 1.

Notes : See *S. clunipes.*



Figs. 55–57—Pupal spiracles of : (55) *Sphegina clunipes* Fall., (56) *Sphegina verecunda* Collin, (57) *Sphegina kimakowiczi* Strobl.

NEOASCIA PODAGRICA Fabricus

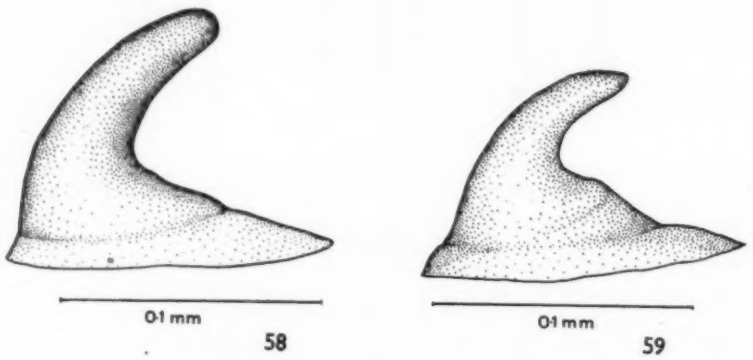
Third instar larva : Length, 6 mm. ; breadth, 1·5 mm. Dorso-ventrally flattened, anterior end truncate, tapering posteriorly from sixth abdominal segment to a telescopic breathing tube (2·5 mm.), eighth abdominal segment elongate. Cuticle yellowish white ; pubescence well developed, short ventrally and on thorax, longer dorsally and especially along lateral ridges ; sparse on seventh and eighth abdominal segments, being confined to a mid dorsal and two lateral bands. Two short heavily sclerotized hooked spines (Fig. 59) dorsally on anterior fold of prothorax. Chaetotaxy as shown in Fig. 8, papillae short except posterior pair of eighth segment which are long. Prolegs weakly developed ; crochets slender, four primaries and five secondaries. Anterior spiracle small with two openings, very similar to *Sphegina clunipes*

(Fig. 51). Posterior spiracle of the eristaline type, with small domed disc, and eight long unbranched plumose terminal setae. Anal papillae simple, 1 : 1 : 2 : 2.

Puparium : Length, 5 mm. ; breadth, 2 mm. Shape as larva but with anterior end rounded and dorsal surface inflated, dark brownish, with bases of spinules darkened ; spiracles 0·5 mm. long, slender (Fig. 60), pale brown.

Taxonomic notes : The larvae of *Neoascia* are the smallest of the saprophytic syrphid larvae and are distinguished by the pair of stout hooks on the prothorax. Not enough is known about the individual species to be able to construct a key. The only certain character separating *podagrica* and *aenea* is the shape and size of the prothoracic hooks, those of *aenea* being distinctly larger. The larvae of *geniculata* and *dispar* (=*floralis* of Lundbeck ; Collin, 1940) are according to Lundbeck (1916) very similar to, and have the same type of pupal spiracles as *podagrica*.

Biological notes : N. podagrica lives in wet decaying manure and is distinctly a farmyard species. There are two generations a year, larvae overwintering and pupating in the spring. These give rise to a summer brood which emerge later in the summer. Nothing much is known about *N. aenea* except that the puparia have been found exposed on *Typha* (reed mace) stems in the early spring. The *Typha* was growing through a floating mat of vegetation.



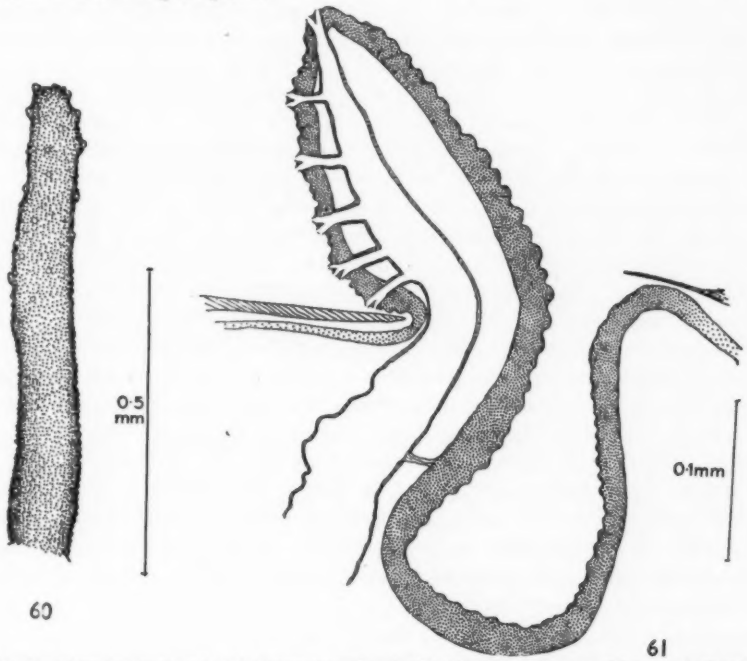
Figs. 58–59—Prothoracic spines of third instar larvae of : (58) *Neoascia aenea* Meig., (59) *Neoascia podagrica* F.

NEOASCIA AENEA Meigen

Third instar larva (based on the puparium) : Length, 7 mm. ; breadth, 1·5 mm. Shape as *N. podagrica*, breathing tube longer (4 mm.). Pubescence scarcely developed, cuticle somewhat warty. Two large heavily sclerotized hooked spines (Fig. 58) on anterior fold of prothorax. Other features as *N. podagrica*.

Puparium : Length, 6 mm. ; breadth, 1·5 mm. Laterally inflated from anus forward ; dorsal surface strongly humped just behind the pupal spiracles for two segments and then rapidly falling away so that the last four segments are distinctly flattened ; opercular region flat and sloping ; cuticle posterior to the anus shrivelled. Cuticle semi-transparent, pale greyish brown with two dark stripes laterally on the dorsal surface. Spiracles (Fig. 61) very short and massive, dark brown, with a large pit anteriorly at the base ; the windows in the puparium through which the spiracles are projected are relatively large.

Notes : See *N. podagrica.*



Figs. 60–61—Pupal spiracles of : (60) *Neoascia podagrica* F., (61) *Neoascia aenea* Meig. sagital section.

KEY TO THE CHRYSOGASTRINI

1. Posterior spiracles transformed into a fine stylet	*Chrysogaster hirtella* (p. 545).
Posterior spiracles not stylet like	2.
2. Densely pubescent, eighth abdominal segment between the last pair of papillae and the preceding pair densely pubescent dorsally (i.e. over 50 spinules present) (Fig. 63)	*C. solstitialis* (p. 544).
Less pubescent, only few (less than 15) spinules between distal pairs of papillae (Fig. 64)	3.
3. Dorsal pubescence moderately well developed, so that more than ten spinules are present in at least one transverse row of each of the second, third and fourth abdominal segments, pubescence noticeably long and dense posteriorly	5.
Dorsal pubescence only weakly developed, maximum number of spinules in transverse rows less than eight, posterior pubescence not noticeably dense	s.g. *Liogaster*....4.

4. Sides of larva with a bold pattern of tubercles, dorsal spinules on abdomen short and fine, half as long as dorsal setae.....	*C.* (*L.*) *splendida* (p. 546).
Sides of larva with a vague pattern of small tubercles, dorsal spinules as long as the dorsal setae	*C.* (*L.*) *metallina* (p. 548).
5. Pubescence weakly developed, spinules finer and not particularly upstanding	*C. splendens* (p. 546).
Pubescence well developed with large and upstanding spinules..	*C. brevicornis* (p. 546).

CHRYSOGASTER SOLSTITIALIS Fallen

Third instar larva : Length, 7 mm. ; breadth, 2 mm. Body more or less cylindrical but somewhat flattened ventrally ; truncate anteriorly with thorax of maximum width, tapering posteriorly from fourth abdominal segment to a short telescopic breathing tube on the eighth abdominal segment ; last segment bears three pairs of lappets. Body deeply corrugated and segments distinct especially ventrally. Cuticle whitish, surface slightly warty ; pubescence well developed on raised folds ; reduction of number of spinules posteriorly accompanied by increase in size of the remainder ; very well developed fringe of spinules along the ventro-lateral line ; pubescence very short ventrally ; eighth abdominal segment densely pubescent, especially dorsally and on the lappets (Fig. 63) ; no tendency for stouter spinules on anterior fold of prothorax. Chaetotaxy as *C. hirtella*, differing in that the lappets bearing lateral sensilla on the eighth segment are very long and slender. Prolegs small anteriorly and becoming even smaller posteriorly so that they are vestigial on A5 and absent on A6 ; seven primary crochets and two other rows on mesothoracic proleg ; five primaries and four secondaries on first abdominal segment, reducing to three weak primaries on the fifth abdominal segment ; crochets at their largest anteriorly ; no anteriorly directed crochets present. Posterior spiracles with strongly rounded disc bearing three pairs of slits ; more or less circular in cross section, with an upstanding fringe of eight short, plumose, terminal setae (Hartley, 1958). Anal papillae as *C. hirtella*.

Puparium : Length, 6 mm. ; breadth, 2·5 mm. Strongly inflated and almost cylindrical about the first six abdominal segments and tapering abruptly behind with the breathing tube bent sharply upwards ; anterior end rounded ; pale brownish and semi-transparent. Spiracles (Fig. 65) pale, 2 mm. long, sinuous, with the end slightly flattened ; finely tuberculate ; raised facets over most of length giving coarser tuberculate effect.

Taxonomic notes : C. solstitialis can readily be distinguished from the two described species of the subgenus *Orthoneura* by the densely pubescent part of the eighth abdominal segment. There are, however, two other species of *Chrysogaster* s.s., and two other species of *Orthoneura* which may confuse the present separation. The two species of *Orthoneura* described here are very difficult to separate even by direct comparison. After pupation determination can be checked by the pupal spiracles as these are distinct for each species.

Biological notes : C. solstitialis overwinters as the larva and has one generation a year, the larvae live in mud containing a large amount of decaying wood and other vegetation at the edge of ponds and streams in woodland areas. *C. brevicornis* and *C. splendens* live in similar places.

CHRYSOGASTER HIRTELLA Loew

Third instar larva : Length, 8 mm. ; breadth, 2·5 mm. Shape (Fig. 62) similar to *C. solstitialis*. Cuticle colourless, slightly warty ; pubescence well developed on ridges only ; fewer, larger spinules posteriorly ; absent or nearly so ventrally ; ventral area bounded by conspicuous fringe of spinules along the ventro-lateral line ; chaetotaxy as shown (Fig. 4) ; prothorax with D4 and D5 separate ; D1 with pair of long setae, others with short rosette of setae ;

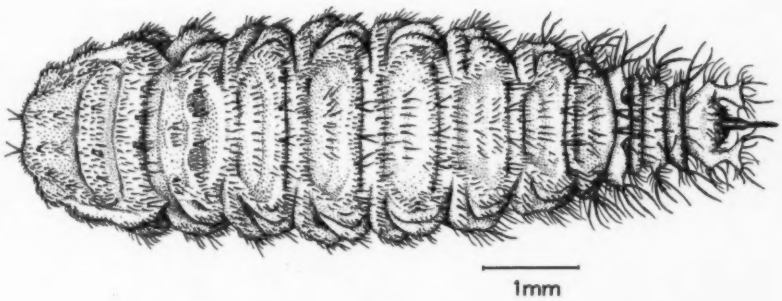


Fig. 62—*Chrysogaster hirtella* Loew, third instar larva, dorsal view.

meso- and metathorax with D1 and D2, D4 and D5, and L1 and L2 all separate. Setae large posteriorly on small papillae except on A8 where the posterior-laterals are on stout, short lappets. Prolegs and crochets as *C. solstitialis*. Posterior spiracles stylet-like (Hartley, 1958) at end of short telescopic breathing tube which can be extended about 2 mm. Anal papillae (Hartley, 1958) much branched and each branch further subdivided into numerous branchlets, formula probably 6 : 6 : 8 : 4.

Puparium : Length, 6 mm. ; breadth, 2·5 mm. Shape as *C. solstitialis* ; spiracles (Fig. 66), up to 2 mm. long, pale, finely tuberculate, slightly curved ; cuticle pale brownish, transparent, with conspicuous dark ring round each spiracular window.

Taxonomic notes : This species is distinct from others of the genus except *C. macquarti* on account of the root-piercing spiracle ; with the adults *C. macquarti* can only be definitely distinguished from *C. hirtella* by the genitalia, and the larvae are probably indistinguishable.

Biological notes : It was known previously that the second and third instars had stylet-like spiracles which are used for piercing roots and obtaining air in this way (Hartley, 1958 ; Varley, 1937 (third instar only)). The first instar also has stylet-like spiracles, 0·2 mm. long with stylet 0·15 mm. The eggs are 1 mm. long and are laid in batches on the underside of vegetation

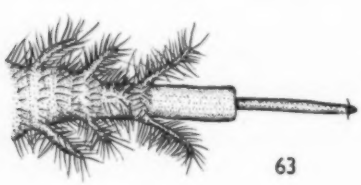
overhanging the breeding place. Probably only one generation occurs in a year, overwintering as larvae. The larvae are associated with various aquatic and semi-aquatic plants including *Glyceria* and *Typha*. The species lives in rich organic mud or silt and has been found near the edges of ponds and slow streams. Pupation takes place on objects raised above water level.

CHRYSOGASTER (*ORTHONEURA*) *BREVICORNIS* Loew

Third instar larva : Length, 9 mm. ; breadth, 2·5 mm. Shape and features as *C. solstitialis*, differing only in the pubescence. Pubescence fairly well developed on raised folds only and in single rows ; spinules upright, large, with tendency to be curved only near tips, numbers in dorsal transverse rows of second and third abdominal segments in two individuals as follows : 8 : 18 : 14, 9 : 24 : 12, and 6 : 21 : 15, 6 : 19 : 12. Eighth abdominal segment with sparse pubescence between the posterior two pairs of lappets, about 14 spinules present mostly ventral (as Fig. 64).

Puparium : Length, 7 mm. ; breadth, 2·5 mm. Shape as *C. solstitialis*, brownish, semi-transparent ; pubescence darkened ; spiracles (Fig. 67) pale, 2 mm. long, sinuate, strongly tuberculate ; facets on distal half especially clumped near end and on raised tubercles.

Notes : See *C. solstitialis*.



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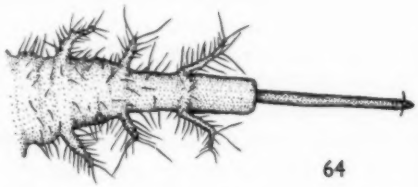

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Figs. 63–64—Dorsal view of posterior ends of third instar larva of : (63) *Chrysogaster solstitialis* Fall., (64) *Chrysogaster splendens* Meig.

CHRYSOGASTER (*ORTHONEURA*) *SPLENDENS* Meigen

Third instar larva : Length, 9 mm. ; breadth, 2·5 mm. Very similar to *C. brevicornis ;* the only difference is that the pubescence is not so stout nor particularly upright having a tendency to be curved near the base.

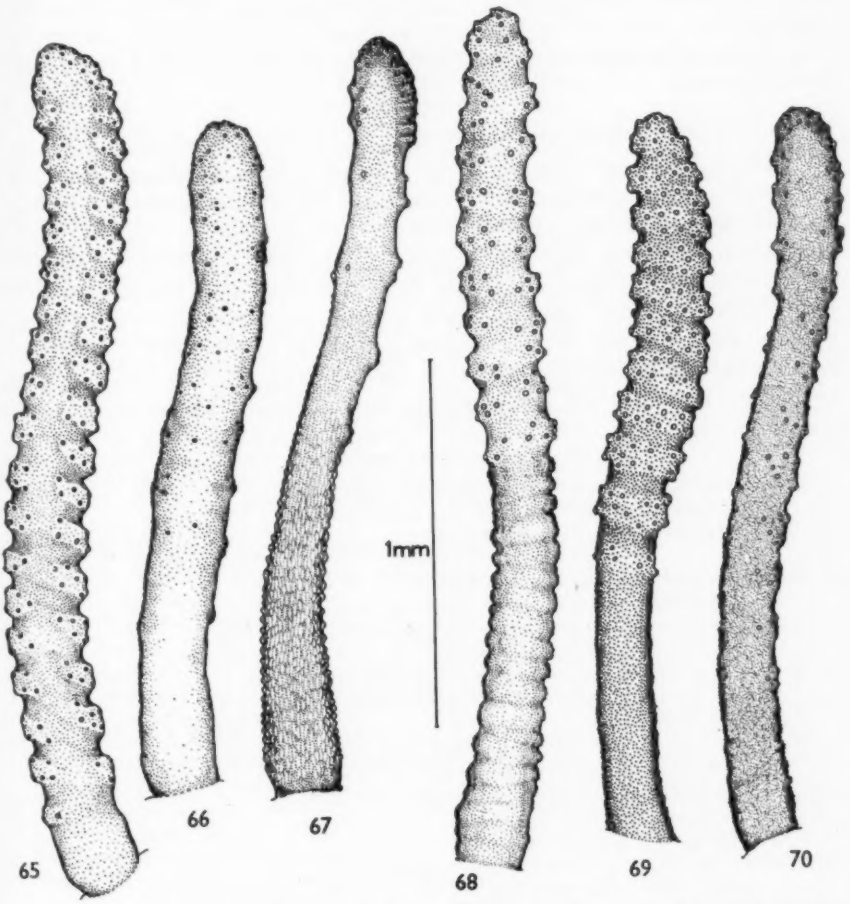
Puparium : Length, 7 mm. ; breadth, 2·5 mm. Shape as *C. solstitialis*, brownish, transparent ; spinules not darkened ; spiracles (Fig. 68) 2·2 mm. long, pale, finely tuberculate ; basal half annulate, facets on distal half.

Notes : See *C. solstitialis*.

CHRYSOGASTER (*LIOGASTER*) *SPLENDIDA* Meigen

Third instar larva : Length, 9 mm. ; breadth, 2·5 mm. Shape and features as *C. solstitialis*, differing only in the form of the cuticle and pubescence. Cuticle distinctly and boldly warty especially on the sides of the larva, warts squarish. Pubescence sparse, numbers of spinules in transverse rows on dorsum of second and third abdominal segments for one specimen as follows : 2 : 5 : 8,

4 : 4 : 5, dorsal pubescence only about half the length of the dorsal setae ; lateral pubescence confined to few spinules around the sensilla and an occasional isolated spinule ; ventro-lateral fringe very well developed ; pubescence absent ventrally ; thoracic pubescence moderately developed, but confined to ridges and anterior prothorax ; conspicuous tuft of long spinules above the fleshy lobes on either side of the mouth.



Figs. 65–70—Pupal spiracles of : (65) *Chrysogaster solstitialis* Fall., (66) *Chrysogaster hirtella* Loew, (67) *Chrysogaster brevicornis* Loew, (68) *Chrysogaster splendens* Meig., (69) *Chrysogaster splendida* Meig., (70) *Chrysogaster metallina* F.

Puparium : Length, 6 mm. ; breadth, 2·5 mm. Shape as *C. solstitialis*, dark brown with wart-like parts paler so that there is a very distinct reticulate effect (Fig. 117) ; spiracles (Fig. 69) 1·8 mm. long, pale, sinuate ; tuberculate on basal half ; facets on distal half in raised annular bands.

Taxonomic notes : The two species of the sub genus *Liogaster* are easily separated from the other species of *Chrysogaster* by their very sparse pubescence, but can only be separated from each other with difficulty ; the difference in the cuticle shows most obviously in the puparium.

Biological notes : The larva of *C. splendida* has been found in the decaying vegetation of a floating mat of *Typha* and other plants in an old pond. There appears to be only one generation a year, overwintering as larvae. Puparium formation occurs in the surface layer of the decaying vegetation just above water level. The eggs are laid in batches on the undersides of leaves just above the mud.

CHRYSOGASTER (*LIOGASTER*) *METALLINA* Fabricus

Third instar larva : Length, 9 mm. ; breadth, 2·5 mm. As *C. splendida* but differing in the wartiness of the cuticle and length of pubescence. Cuticle only slightly warty, warts small and elongate dorso-ventrally, poorly defined. Pubescence on dorsum nearly as long as the dorsal setae, numbers of spinules in the transverse rows of the second and third abdominal segments of one specimen as follows : 4 : 4 : 7, 2 : 7 : 6.

Puparium : Length, 6 mm. ; breadth, 2·5 mm. Shape as *C. solstitialis*, brown with vague markings (Fig. 116) ; spiracles (Fig. 70) 1·8 mm, long, pale brown, fine pattern of small narrow tubercles ; facets along most of length.

KEY TO THE ERISTALINI

1. Pubescence absent on dorsum of last six abdominal segments ; sensilla conspicuous each with 10–15 setae radially arranged ; anterior spiracle long and pointed (Fig. 85) ..... *Mallota cimbiciformis* (p. 562).

—. Pubescence present on dorsum of abdominal segments ; or if absent dorsally some anteriorly directed crochets between last pair of prolegs ; sensilla inconspicuous each with less than eight setae ..... 2.

2. Abdominal prolegs with stout well sclerotized crochets in two distinct semicircular rows ; anterior spiracle pale brownish (Fig. 84) ..... *Myiatropa florea* (p. 564).

—. Abdominal prolegs with crochets in more than two distinct rows, which are not semicircular on first three abdominal segments ; if crochets tend to be in only two rows, the anterior spiracles are dark brown..... 3.

3. Tracheal trunks undulating, with either
   (*a*) crochets on abdominal prolegs in three to four very distinct rows, with more than ten very long crochets in primary row..... *Helophilus* group I....11.
   (*b*) or with double row of anteriorly directed crochets between the sixth abdominal prolegs and confluent with the crochets on these prolegs..... *Helophilus* group II....12.

—. Tracheal trunks straight ; crochets on abdominal prolegs in two to three distinct rows, with five to nine crochets in primary row or, if more than ten, pubescence sparse and as short black spines ; if anteriorly directed crochets present on sixth abdominal segment between the prolegs they are well separated from the prolegs..... *Eristalis*....4.

4. Anteriorly directed crochets in short double row just in front of the sixth abdominal prolegs ..... 5.
—. Without crochets in front of sixth abdominal prolegs..... 6.
5. With seven to nine larger crochets in posterior row of the above series ..... *E. sepulchralis* (p. 550).
—. With only five larger crochets in posterior row of the above series *E. aeneus* (p. 552).
6. Cuticle with reticulate pattern of brown patches..... *E. nemorum* (p. 556).
—. Cuticle without reticulate pattern of brown patches..... 7.
7. Primary crochets stout and strongly hooked, about as long as wide with distal two fifths strongly sclerotized (Fig. 74) ; (anterior spiracle short with broadly rounded recurved tip (Fig. 82) *E. tenax* (p. 553).
—. Primary crochets long and slender, weakly hooked, nearly twice as long as wide, with distal quarter or less weakly sclerotized (Fig. 73)..... 8.
8. Anterior spiracle when viewed postero-laterally elongate with a narrow triangular tip, dark brownish..... 9.
—. Anterior spiracle short with a broadly truncate end (Fig. 79) pale brownish ..... *E. intricarius* (p. 554).
9. Anal papillae with 20 branches (Fig. 21). Anterior spiracle (Fig. 80) with lower part of facet band running horizontally around the spiracle for half the circumference with the facets directed slightly upwards ; spiracle abruptly narrower above this band and curved outwards ; face of spiracle generally rounded, apex straight ..... *E. pertinax* (p. 552).
—. Anal papillae with 24 branches (Fig. 22). Anterior spiracle (Fig. 81) with the lower part of facet band acutely angled with the upright part, lower band only extending around for about one-third of the circumference ; facets of lower band directed outwards ; spiracle gradually tapering to apex above this band, and curved slightly backwards ; face of spiracle flattened, apex slightly hooked..... 10.
10. Pubescence on dorsum of abdomen and between prolegs grouped into short transverse lines of two or three spinules..... *E. abusivus* (p. 557).
—. Pubescence not grouped..... *E. arbustorum* (p. 556).
11. Crochets of sixth abdominal prolegs with crochets on one proleg separated from crochets of opposite proleg by a distance greater than maximum crochet in length. A conspicuous tuft of long spinules just behind the anus which are as long as the adjacent papillae..... *H. pendulus* (p. 557).
—. Crochets of sixth abdominal prolegs almost confluent, separated by less than half maximum crochet length. Only few short spinules in tuft just behind anus ..... *H. hybridus* (p. 558).
12. Anterior spiracles dark brown, elongate ; (pubescence often reduced and replaced by small tubercles)..... *H. lineatus* (p. 561).
—. Anterior spiracles pale yellow-brown, short..... 13.
13. Papillae bearing most posterior sensilla at distal end of the tail as long as the diameter of the first, or basal, segment of the breathing tube ..... 14.
—. Papillae bearing most posterior sensilla at distal end of tail less than half as long as the diameter of the basal segment of the breathing tube..... 15.
14. Anterior spiracle straight with a broad truncate end (Fig. 87).. *H. versicolor* (p. 559).
Anterior spiracle with a narrow slightly hooked end (Fig. 88).. *H. frutetorum* (p. 559).
15. Crochets with at least distal quarter solidly sclerotized (Fig. 89)..... *H. transfugus* (p. 560).
Crochets with only the tip solidly sclerotized (Fig. 90) ..... *H. lunulatus* (p. 561).

ERISTALIS SEPULCHRALIS Linnaeus

Third instar larva : Length, 20+15 mm. ; breadth, 4 mm. Body (Fig. 71) approximately cylindrical ; anterior end truncate ; last two segments abruptly tapering to form a long tail sheathing a long telescopic breathing tube, which can be extended several times body length ; no lappets present. Cuticle semi-transparent becoming opaque whitish with age, larva generally whitish ; pubescence moderately developed, fairly long and slender ; longer on ridges, especially laterally ; prothoracic spinules stouter, short, slightly hooked, not particularly sclerotized ; conspicuous tuft of long spinules on dorsal lip above mouth. A double row of slender, anteriorly directed spines in front of the sixth abdominal prolegs and distinct from them ; eight to ten larger spines in

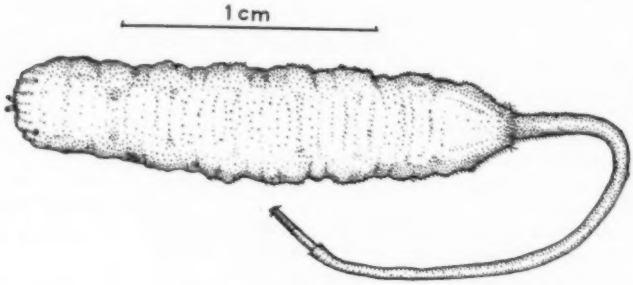


Fig. 71—*Eristalis sepulchralis* L., third instar larva, dorsal view.

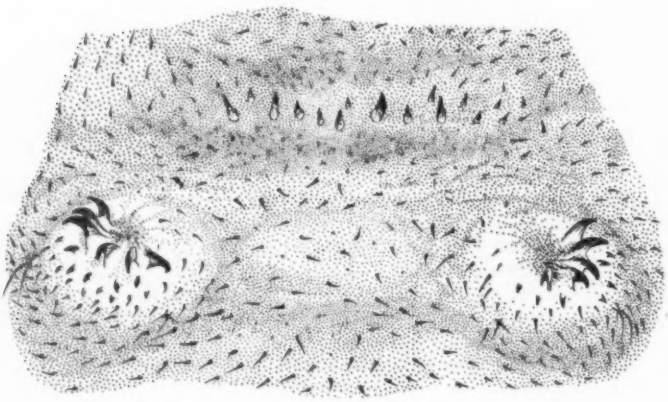


Fig. 72—*Eristalis sepulchralis* L., third instar larva, ventral side of sixth abdominal segment showing the sixth pair of abdominal prolegs and in front of them the anteriorly directed spines.

the posterior row (Fig. 72). Prolegs well developed ; crochets slender, weakly sclerotized ; in two principal rows, 6 in first. Chaetotaxy as shown (Fig. 3), sensilla on small papillae ; setae long and slender, up to three times length of pubescence ; the VL sensilla very close together. Anterior spiracle (Fig. 76)

brownish, slightly curved ; facets distinctly bordered, in double row with the face of the spiracle entirely obliterated. Posterior spiracle pale, similar to *E. tenax* (Fig. 75) ; terminal setae simple, plumose. Anal papillae simple, formula 1 : 1 : 2 : 2 (Fig. 19).

Puparium : Length, 10 mm. ; breadth, 4 mm. Light brown speckled with black, pubescence not darkened ; inflated dorsally and somewhat flattened ventrally with anterior end concave ; anterior larval spiracles strongly protruded ; pupal spiracles (Fig. 93) 3 mm. long, slightly curved, facets dorsal and lateral on distal half.

Taxonomic notes : The larvae of *Eristalis* are generically very distinct although *Myiatropa florea* might be confused with them. They have characteristically dilated straight tracheal trunks and characteristic retractable prothoracic spiracles. The two species *E. sepulchralis* and *E. aeneus* differ from the rest of the genus by possessing a double row of anteriorly directed crochet-like spines on the ventral side of the sixth abdominal segment slightly forward of the prolegs ; *E. sepulchralis*, and possibly *E. aeneus*, also differs in the form of the anal papillae, which are simple unbranched. *E. sepulchralis* can be distinguished from *E. aeneus*, by the prothoracic spiracles and that the former has more of the anteriorly directed crochet-like spines mentioned above.

The remainder of the genus are more difficult to identify. *E. arbustorum* and *E. abusivus* both have anal papillae in which the first tube has two small side branches, the other species have only one long side branch on the first tube. The shape of the prothoracic spiracles is a sure way of separating *E. tenax*, *E. pertinax*, *E. intricarius* and *E. nemorum* although the latter can be distinguished at once by the appearance of the cuticle. *E. arbustorum* and *E. abusivus* are very similar in all respects except that the three specimens of *E. abusivus* examined had their dorsal pubescence grouped in twos and threes transversely while the pubescence of *E. arbustorum* is normally distributed.

Biological notes : The larvae of *E. sepulchralis* have been found commonly in ponds with a large amount of decaying vegetation but with little sewage contamination. They have, however, been noted on one occasion in some pools on the edge of an estuarine marsh where there was some seepage of sewage, and a few larvae have been found in a farmyard drain. The eggs are laid on anything just above the habitat in clusters of up to a hundred. There are at least two broods a year, possibly more ; the larvae overwinter and pupate early in the spring. Eggs have been found from May onwards. The larvae have, at hatching, only slightly dilated tracheal trunks except in the region of the sixth abdominal segment where there is a bulb-like swelling ; the normal dilation is found before the first moult. All the crochets are conspicuous in the first instar. The tail is very short at first but lengthens during first instar growth, the breathing tube is likewise short. Time of development depends on temperature and richness of food supply. In summer from egg to adult may take four to eight weeks. The egg stage lasts about two days and the puparium period about ten days. Pupation occurs in detritus a little way above water level.

ERISTALIS AENEUS Scopoli

Third instar larva : Length, 20+15 mm. ; breadth, 4 mm. Shape as *E. sepulchralis*. Larva whitish ; pubescence moderately well developed, fairly long dorsally and on lateral ridges, short and weakly developed ventrally, stouter spinules present on anterior prothorax. A short double row of anteriorly directed crochet-like spines, on the ventral side of the sixth abdominal segment and in front of the prolegs, five or six of the posterior row being much larger than the others. Prolegs well developed ; crochets well sclerotized, in three rows with six primaries. Chaetotaxy as *E. sepulchralis*. Anterior spiracles (Fig. 77) brown, slightly recurved ; facets all over face, morula-like. Posterior spiracles pale, similar to *E. tenax :* terminal setae simple, plumose.

Puparium : Length, 11 mm. ; breadth, 4 mm. As *E. sepulchralis ;* pupal spiracles had not yet been produced in the specimen examined.

Taxonomic notes : See *E. sepulchralis*.

Biological notes : The larva of this species has been found in pools containing rotting seaweed on the seashore. The larvae have been found in August and September and adults have been found hibernating in buildings, this suggests that like *E. tenax* this species overwinters as the adult and has two larval generations during the summer.

ERISTALIS PERTINAX Scopoli

Third instar larva : Length, 25+15 mm. ; breadth, 6 mm. Shape as *E. sepulchralis*. Cuticle whitish ; pubescence well developed, short and fine ; little lateral variation ; stout and well sclerotized on anterior prothorax. Prolegs well developed ; crochets (Fig. 73) long and stout in two principal rows, six in first, backed by several rows of stout spinules ; sixth abdominal prolegs with three outer crochets anteriorly directed. Segmental setae short, arrangement as *E. sepulchralis*. Anterior spiracle (Fig. 80) dark, upright ; with facets extending more than half-way round basally so that all the facets cannot be seen from one position, distinctly narrower above this. Posterior spiracle lightly and uniformly sclerotized, terminal setae simple, plumose. Anal papillae branched, as *E. tenax*, formula 2 : 2 : 4 : 2.*

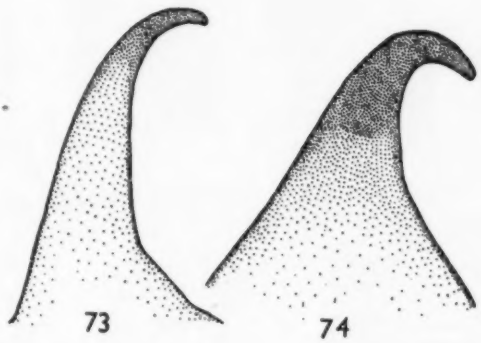
Puparium : Length, 15 mm. ; breadth, 6 mm. Shape very similar to *E. arbustorum*, brown with darker blotches, pubescence darkened ; spiracle 3·5 mm. long, with openings along the greater part of its length (Fig. 92).

Taxonomic notes : See *E. sepulchralis*.

Biological notes : Larva of *E. pertinax* have been found in the rich organic sludge found in farmyard drains, in very wet manure, occasionally in ponds with a large amount of decaying vegetation, and in sodden sawdust of an old sawpit ; (the latter situation is water sodden sawdust at least forty years old. There is no sewage pollution but cattle roam over it. Also found in this place were the larvae of *Helophilus pendulus.*) *E. pertinax* overwinters

* Not 1 : 1 : 3 : 2 as stated by Gäbler (1932).

as the larval stage and there is one summer brood. This species is the first of the farmyard species to emerge in the spring and the first to lay eggs. Eggs are laid in crevices of overhanging objects. The puparium is partially buried in drier material a short distance from larval habitat.



Figs. 73–74—Primary crochets of third instar larvae of : (73) *Eristalis pertinax* Scop., (74) *Eristalis tenax* L.

ERISTALIS TENAX Linnaeus

Third instar larva : Length, 23+15 mm. ; breadth, 5 mm. Shape as *E. sepulchralis*. Cuticle whitish ; pubescence well developed but fairly short ; spinules on prothorax stout with strongly sclerotized tips ; no particular differentiation of lateral spinules. Prolegs well developed ; crochets (Fig. 74) large and stout with strongly sclerotized hooks in two principal rows, 7 in first, backed by stout spinules ; three outer crochets of the sixth abdominal proleg anteriorly directed. Chaetotaxy as *E. sepulchralis* but with the setae shorter, borne on very small tubercles. Anterior spiracle (Fig. 82) very dark, short, stout, and curved backwards ; with 21 facets. Posterior spiracles (Fig. 75) with distal two thirds brownish, terminal setae with a tendency to be branched. Anal papillae branched, formula 2 : 2 : 4 : 2 (Fig. 21).

Puparium : Length, 13 mm. ; breadth, 6 mm. Greyish brown often paler ventrally ; inflated laterally, anterior end rounded ; pupal spiracles projecting forward and then bending sharply downward, little more than 1 mm. long ; very dark, openings mainly on the dorsal (posterior) surface (Fig. 98).

Taxonomic notes : See *E. sepulchralis*.

Biological notes : Contrary to a statement by Gäbler (1930) this species does not overwinter as a larva, in this country at least. The adults hibernate and start flying again in the spring, eggs are not laid until the end of May and take two days to hatch. Under good conditions the larval period takes about eighteen days and the adults emerge about ten days later. A second brood is produced later in the summer and this gives rise to the autumn adults which later hibernate. One female after being captured laid three hundred eggs and

was found to contain over four hundred developing eggs in her ovaries afterwards. There is a very high mortality among the first instar larva from failure to reach a suitable part of the habitat. *E. tenax* only breeds in farmyard drains and other places of very high animal sewage content including putrefaction around carcases (see Osten-Sacken, 1894, on the Ox-born Bee of Biblical fame).

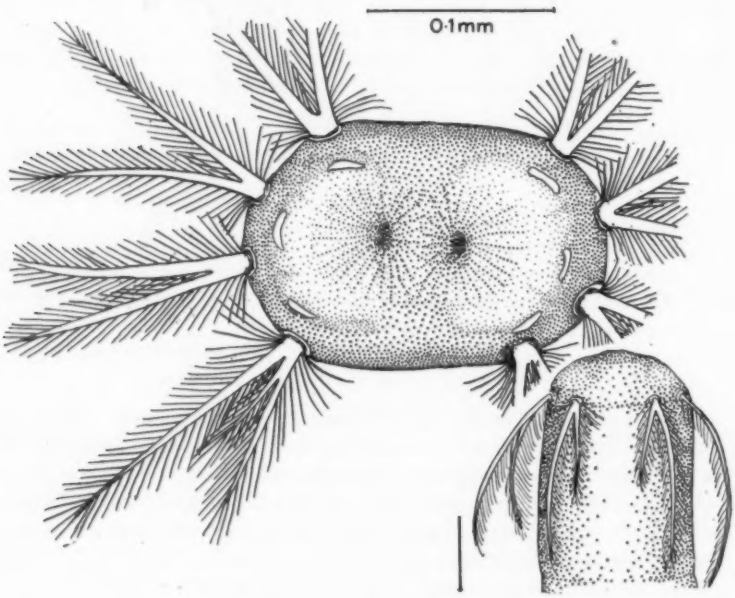
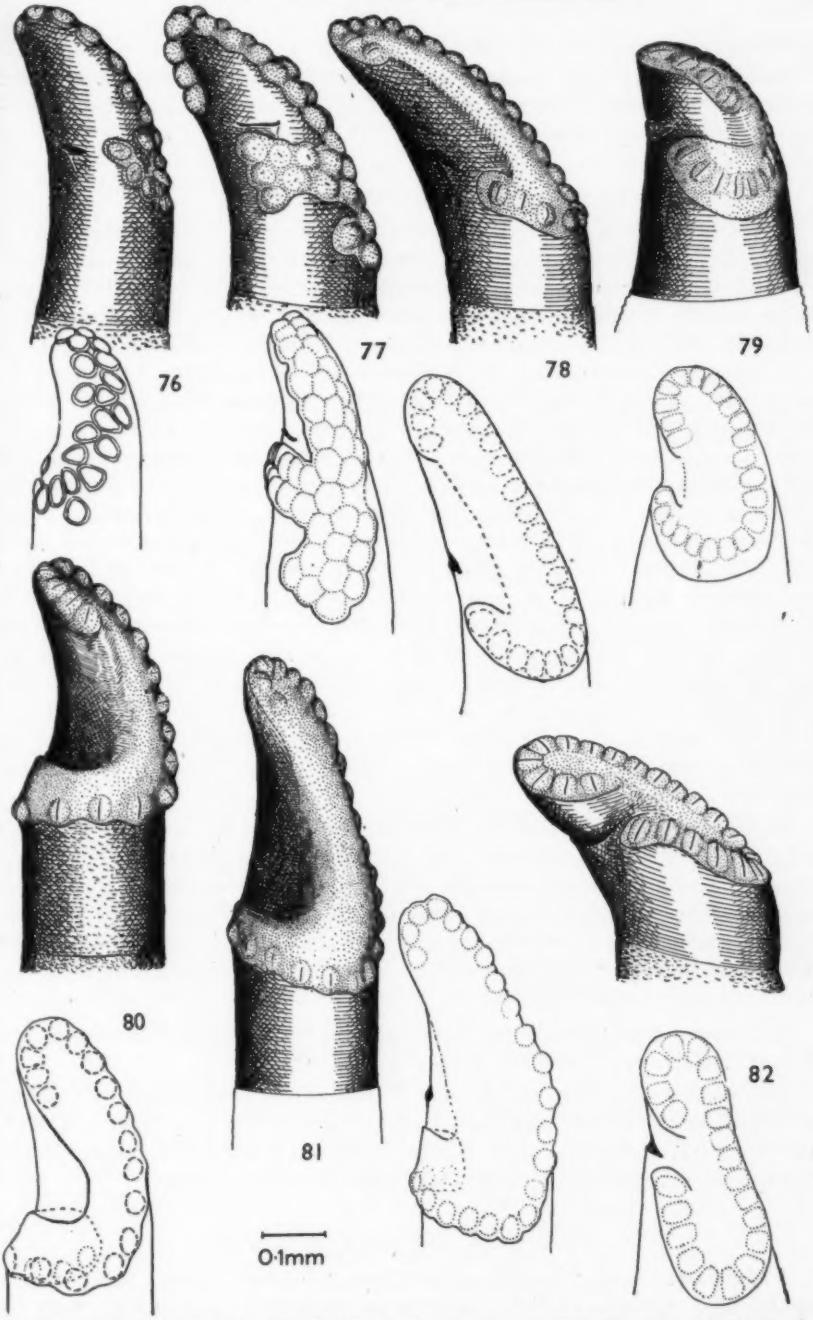


Fig. 75—*Eristalis tenax* L., third instar larva, posterior spiracles.

ERISTALIS INTRICARIUS Linnaeus

Third instar larva : Length, 23+15 mm. ; breadth, 5 mm. Shape as *E. sepulchralis*. Cuticle whitish ; pubescence short and dense, especially dorsally where it is developed even in the furrows of the cuticle ; prothoracic spinules stouter and recurved ; lateral ridge spinules slightly longer. Prolegs well developed ; crochets in two principal rows, seven in first, large and slender ; three outer crochets on sixth abdominal proleg directed anteriorly. Chaetotaxy as in *E. sepulchralis* but with a greater separation of VL1 and VL2. Anterior spiracles (Fig. 79) light brown and shining, stout and shortly conical ; up to 24 facets. Posterior spiracles moderately sclerotized, terminal setae simple. Anal papillae, branched, similar to *E. tenax*, formula 2 : 2 : 4 : 2.

Puparium : Length, 13 mm. ; breadth, 5 mm. Brownish with blackening of the spinules ; rounded anteriorly and not noticeably inflated. Pupal spiracles pale brown, projecting antero-dorsally, 2·5 mm. long, nearly straight, facets laterally on distal third (Fig. 94).



Figs. 76–82—Prothoracic spiracles of third instar larvae of: (76) *Eristalis sepulchralis* L., (77) *Eristalis aeneus* Scop., (78) *Eristalis nemorum* L., (79) *Eristalis intricarius* L., (80) *Eristalis pertinax* Scop., (81) *Eristalis arbustorum* L., (82) *Eristalis tenax* L.

Taxonomic notes : See *E. sepulchralis.*

Biological notes : This species has a very similar life history to *E. pertinax.* The larvae have been found in ponds with a large amount of decaying vegetation and in farmyard drains.

ERISTALIS NEMORUM Linnaeus

Third instar larva : Length, 20+12 mm. ; breadth, 5 mm. Shape as *E. sepulchralis.* Cuticle whitish with reticulate pattern of heavily sclerotized brownish patches almost absent ventrally and becoming very distinct and darker dorsally, where they resemble crocodile skin ; on the dorsal surface the separation between the patches is abruptly decreased so that the general appearance is a greyish white larva with a dark brown zigzag region on the dorsal side. The pubescence is sparse and represented by small very dark spinules each arising from the centre of a brown patch. Anterior spinules weak ; no particular differentiation of the laterals ; pubescence on dorsal side of abdomen confined to single rows on transverse ridges. Tail bare except for weakly developed row of minute spinules laterally. Prolegs well developed with two principal rows of crochets. Crochets relatively slender with black tips. Usually ten crochets in principal row, of which the outer three or four are directed anteriorly on abdominal prolegs 2–6. Chaetotaxy as *E. sepulchralis ;* sensilla sessile, except those of abdominal segment 7 which are on short papillae, surrounded by a group of slender spinules ; the setae are fine and numerous (five or more) except L3 and VL2 which have only two setae. Anterior spiracles (Fig. 78) brown and moderately shining, 21 facets all in the same plane. Posterior spiracles with dark disc and pale sides, plumose terminal setae simple. Anal papillae branched, similar to *E. tenax* formula 2 : 2 : 4 : 2.

Puparium : Length, 13 mm. ; breadth, 6 mm. Not particularly inflated and slightly flattened dorso-ventrally ; anterior end almost square, with pupal spiracles protruding from the upper angle. Cuticle darkened all over so that the reticulate pattern and prominent dorsal markings are difficult to see. Pupal spiracles dark, 2·5–3 mm. long, with a slight twist, most obvious when viewed from behind ; facets mainly at tip and extending half way along the ventral (anterior) side (Fig. 95).

Taxonomic notes : See *E. sepulchralis,* this larva is quite distinct on account of its cuticular markings in any case.

Biological notes : The life history of this species is probably very similar to *E. pertinax.* Larvae have been found overwintering in a farmyard drain, and young larvae, in September, in a pool contaminated with cattle droppings. The species emerges about three weeks later than *E. pertinax.*

ERISTALIS ARBUSTORUM Linnaeus

Third instar larva : Length, 20+12 mm. ; breadth, 5 mm. Shape as *E. sepulchralis.* Cuticle whitish ; pubescence well developed, fairly short but longer on ridges ; weakly developed and shorter ventrally ; spinules with a

slight greyish tinge, those on the prothorax only weakly developed and lightly sclerotized. Prolegs well developed ; crochets in two principal rows, six or seven in first, slender, tips lightly sclerotized ; sixth abdominal proleg with three outer crochets anteriorly directed. Chaetotaxy as *E. sepulchralis*. Anterior spiracle (Fig. 81) elongate with the tip curved inward ; all 22 facets just visible at once from the side ; spiracle dark and shining. Posterior spiracle lightly sclerotized, terminal setae simple. Anal papillae branched as shown (Fig. 22), formula 3 : 3 : 4 : 2.

Puparium : Length, 11 mm. ; breadth, 5 mm. Brown with darkened pubescence, inflated laterally with larval spiracles greatly protruded ; pupal spiracles 3 mm. long, straight with openings on distal two thirds (Fig. 97).

Taxonomic notes : See *E. sepulchralis*.

Biological notes : The life history of this species is very like that of *E. pertinax* but it is about two weeks later in appearance. It seems to be restricted to water with a high degree of animal pollution such as farmyard drains and has also been found in temporary pools which contain cow droppings. Egg laying has been observed as late as October.

ERISTALIS ABUSIVUS Collin

Third instar larva : Length, 20+12 mm. ; breadth, 5 mm. Very similar in all respects to *E. arbustorum* excepting the dorsal pubescence. Dorsal pubescence well developed, short ; on the abdominal segments the spinules are in short transverse rows of two's and three's ; lateral pubescence normal, not particularly dense ; ventral pubescence sparse, very short, and with a tendency to be clumped as dorsally.

Puparium : Length, 11 mm. ; breadth, 5 mm. As *E. arbustorum* but differing in the spiracles, which are 2·5 mm. long, with distinct spiral twist (Fig. 96).

Taxonomic notes : See *E. sepulchralis*.

Biological notes : Four larvae were found in the mud at the edge of a moorland pond on the Mendips in September, these were kept in the laboratory, pupated in October and emerged in November, but under natural conditions these would probably have pupated in the following spring.

HELOPHILUS PENDULUS Linnaeus

Third instar larva : Length, 19+10 mm. ; breadth, 4·5 mm. Shape typical Eristaline with a prominent lateral lappet on each side of the seventh abdominal segment at the base of the tail, and two more pairs of lappets ventro-laterally behind the anus. Cuticle whitish ; pubescence well developed, short, longer posteriorly on lateral folds. Very long and dense on lappets, and in large tuft just behind the anus ; spinules on anterior prothorax short, moderately stout and sclerotized, slightly hooked, and extending back only as far as the anterior dorsal sensilla. Chaetotaxy as *Eristalis sepulchralis* with VL1 & 2 of A7 on the first lappet, 7 of A8 on the second, and A7 L1 on the third ; setae as *E. sepulchralis* with a more elongate seta in D2 and L1, L3 with single very

long seta which is often broken off. V2 very inconspicuous. Prolegs very wide but short, those on A6 very close together. Crochets very numerous, with about 12 primaries on thoracic prolegs and many smaller crochets covering the posterior side of the proleg ; primary crochets long and slender ; others stouter and more strongly sclerotized ; the first five pairs of abdominal prolegs similar but with fewer rows ; A6 with fourteen primaries, approximately five rows, mainly anteriorly directed ; crochets not extending up the inside of the prolegs. Anterior spiracles (Fig. 86) completely retractile, pale, short, with about twelve facets. Posterior spiracles dark, similar to *E. tenax* (Fig. 75) with very short flat cap. Tracheal trunks undulating. Anal papillae simple, formula 1 : 1 : 2 : 2 (as Fig. 19).

Puparium : Length, 11 mm. ; breadth, 5 mm. Inflated laterally, rounded at ends ; lappets greatly shrunk ; cuticle dark brown ; pubescence darkened, almost black ; spiracles (Fig. 100) light brown.

Taxonomic notes : The species of the *H. pendulus* group are very similar and quite distinct from the other species of *Helophilus*. They are at once distinguished by the four rows of numerous long crochets, the presence of lappets on the body, and their greater size. *H. pendulus* can only be separated satisfactorily from *H. hybridus* by the spinules. *H. pendulus* has a conspicuous tuft of long spinules just behind the anus and around the lappets, the spinules are also longer than the lappets and tend to mask them ; in *H. hybridus* these spinules are much less dense and scarcely longer than the lappets. The *Eristalis* illustrated by Miall (1895) is in fact one of this group.

Biological notes : Larvae of *H. pendulus* have been found in farmyard drains, very wet manure in wet decomposing silage, and in very old wet sawdust. The larvae overwinter and there is a second generation during the summer.

HELOPHILUS HYBRIDUS Loew

Third instar larva : Length, 19+10 mm. ; breadth, 4·5 mm. Shape as *H. pendulus*, the three lateral lappets are less prominent. Pubescence well developed, short, only slightly longer on lateral folds ; pubescence on lappets and post-anal tuft only slightly longer than that on the lateral folds and not particularly dense. Crochets of A6 prolegs extending up the inside of the prolegs and almost meeting on the mid-ventral line. Anterior spiracles stouter than *H. pendulus*. Posterior spiracles only moderately sclerotized with a darker band two thirds from base, the whole spiracles becoming darker with approach of puparium formation. Other features as *H. pendulus*.

Puparium : Length 12 mm. ; breadth, 4 mm. Radially rather than laterally inflated ; cuticle medium brown ; pubescence slightly darkened. Spiracles 1·7 mm. long, yellow brown with facets on distal two thirds (Fig. 101).

Taxonomic notes : See *H. pendulus*.

Biological notes : This species has been found breeding in a pond with a dense growth of *Typha* (reed mace). The larvae feed particularly in the decaying rhizomes. Eggs are laid in batches on stems and leaves just above

the water. The first instar larvae do not have the characteristic undulating dilated tracheal trunks but these develop by the second instar. The crochets are very distinct with black tips. The larvae overwinter, and eggs are laid from May onwards. There is probably a second generation later in the summer.

HELOPHILUS VERSICOLOR Fabricius

Third instar larvae : Length, 16+10 mm. ; breadth, 4 mm. Shape typical Eristaline and without development of lateral lappets on A7. Cuticle semi-transparent to whitish, sometimes with a slight pinkish tinge ; pubescence well developed, short, slightly longer on ventro-lateral lines ; spinules on anterior prothorax slightly sclerotized, little stouter than pubescence, and weakly hooked. Chaetotaxy as *H. pendulus* ; setae generally small ; papillae small ; posterior pair on the tail on slender, elongate lappets, at least as long as the diameter of the first segment of the breathing tube ; each bearing on the apical sensillum a pair of equally long setae (as Fig. 91). Prolegs small ; crochets long and slender, as *H. lunulatus* (Fig. 90) ; in two very distinct rows and numerous smaller accessories, extending up the inside of the abdominal prolegs, crochets on sixth abdominal prolegs mainly anteriorly directed, and extending up the inside of the prolegs to become confluent with crochets of the other side. Anterior spiracles (Fig. 87) pale yellowish, apex broadly truncate and only very slightly recurved. Posterior spiracles similar to *H. pendulus*, moderately sclerotized.

Puparium : Length, 11 mm. ; breadth, 4 mm. Distinctly flattened ; anterior end abruptly rounded ; posterior end tapering behind the anus ; semi-transparent brownish ; pupal spiracles (Fig. 103) 1·5 mm. long, slightly curved, protruding anteriorly and not rising dorsally above the puparium, pale brownish yellow ; facets along distal half.

Taxonomic notes : The larvae of the *H. versicolor* group are very similar and can only be separated with difficulty. The long lappets at the end of the tail distinguish *H. versicolor* and *H. frutetorum* from *H. transfugus* and *H. lunulatus* quite satisfactorily but further separation can only be certain by comparison. The puparia can be distinguished more readily.

Biological notes : The larvae of *H. versicolor* have been found in ponds where there is a large amount of *Typha*. There seems to be only one generation a year, the larvae overwinter and pupate in late spring. The normal place for puparium formation is in between the leaf bases of *Typha* and it is notable in this respect that the puparium is always slightly flattened and the spiracles project forwards and not upwards even when the puparium is formed in the open. The species seems to be particularly vulnerable to parasitism by the proctotrupoid *Diapria conica* F. infection presumably occurring as the larvae leave the water.

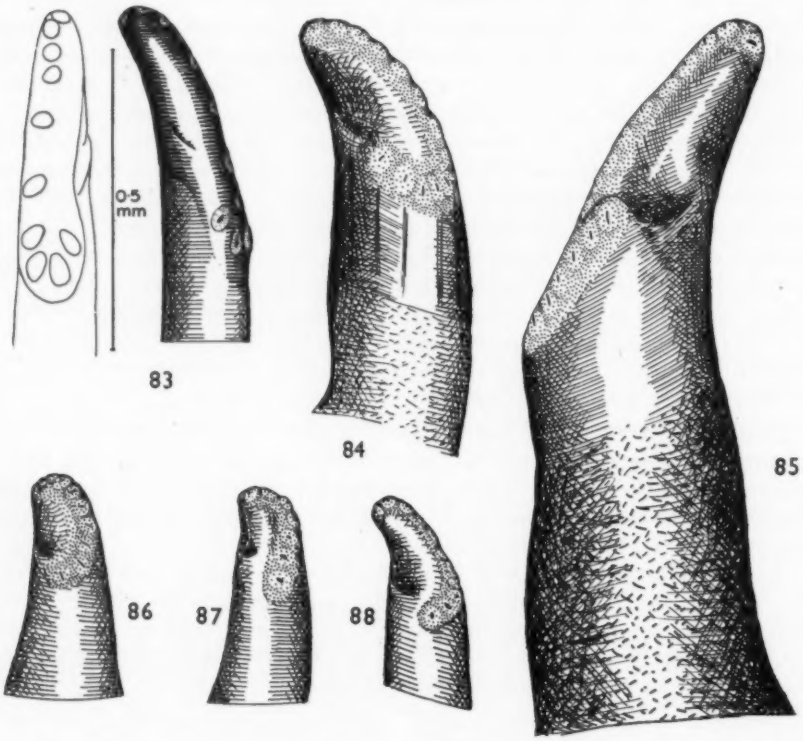
HELOPHILUS FRUTETORUM Fabricius

Third instar larva : The larva is identical with *H. versicolor* except for the prothoracic spiracles. Prothoracic spiracle pale yellowish, apex narrowly rounded and distinctly recurved (Fig. 88).

Puparium : Length, 10 mm. ; breadth, 3·5 mm. More or less cylindrical, rounded at the ends ; pupal spiracles 2 mm. long, projecting dorso-anteriorly, yellow brown ; facets clumped on distal quarter (Fig. 102).

Taxonomic notes : See *H. versicolor*.

Biological notes : There is probably only one generation a year, the larvae overwinter and have been found in rich organic mud of a woodland pond.



Figs. 83–88—Prothoracic spiracles of third instar larvae of : (83) *Helophilus lineatus* F., (84) *Myiatropa florea* L., (85) *Mallota cimbiciformis* Fall., (86) *Helophilus pendulus* L., (87) *Helophilus versicolor* F., (88) *Helophilus frutetorum* F.

HELOPHILUS TRANSFUGUS Linnaeus

Third instar larva : The larva is very similar to *H. versicolor* except that the posterior papillae on the tail are almost sessile, the associated setae are long and slender. Crochets with distal third solidly sclerotized (Fig. 89).

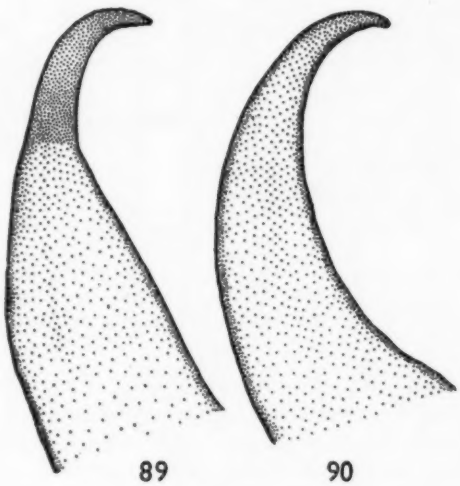
Puparium : Length, 10 mm. ; breadth, 4 mm. Very similar to the puparium of *H. frutetorum* excepting the larval differences and the pupal spiracles (Fig. 105).

Taxonomic notes : See *H. versicolor*.

Biological notes : A solitary larva about to pupate was found in May in a woodland pond. The larva was found in a leaf base of *Typha* but the puparium is not flattened or otherwise modified.

HELOPHILUS LUNULATUS Meigen

Third instar larva : The larva is very similar to the larva of *H. versicolor* but with the posterior pair of papillae on the breathing tube very much reduced, setae long and slender. Crochets with only extreme tip sclerotized (Fig. 90).



Figs. 89–90—Primary crochets of the third instar larvae of : (89) *Helophilus transfugus* L., (90) *Helophilus lunulatus* Meig.

Puparium : Length, 10 mm. ; breadth, 4 mm. Shape and appearance as *H. frutetorum ;* pupal spiracles (Fig. 104).

Taxonomic notes : See *H. versicolor.*

Biological notes : A mature larva of this species was found in early June in a pond with a dense stand of *Typha.*

HELOPHILUS LINEATUS Fabricius

Third instar larva : Length, 10+8 mm. ; breadth, 3 mm. Shape as *H. versicolor.* Cuticle whitish ; pubescence colourless, short, sparse ; patchy on abdomen with small tubercles replacing the spinules ; anterior prothoracic spinules stouter often with branched ends. Chaetotaxy as *E. sepulchralis* ; papillae small and inconspicuous except last pair on tail which are elongate (Fig. 91). Crochets pale, slender, in two principal rows, usually six in first ; numerous anteriorly directed spines in double row between the prolegs of sixth abdominal segment and confluent with the crochets on them which are also mainly anteriorly directed. Anterior spiracles (Fig. 83) relatively long

and narrow, with a slight outward curve ; dark and shining, usually 11 facets well separated. Posterior spiracles dark except cap and basal fifth. Anal papillae simple, formula 1 : 1 : 2 : 2.

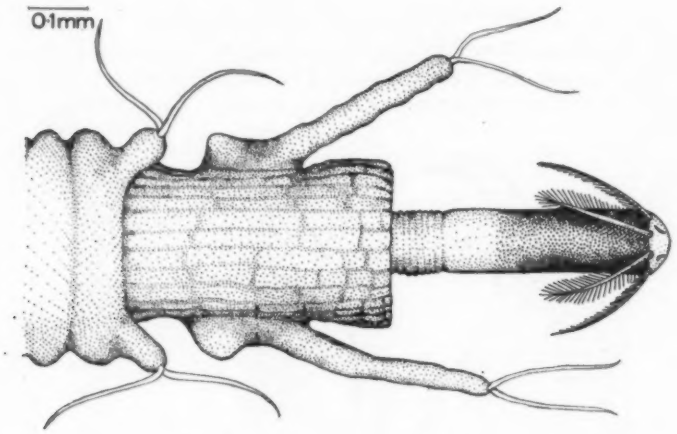


Fig. 91—*Helophilus lineatus* F., third instar larva, posterior end of tail with breathing tube retracted.

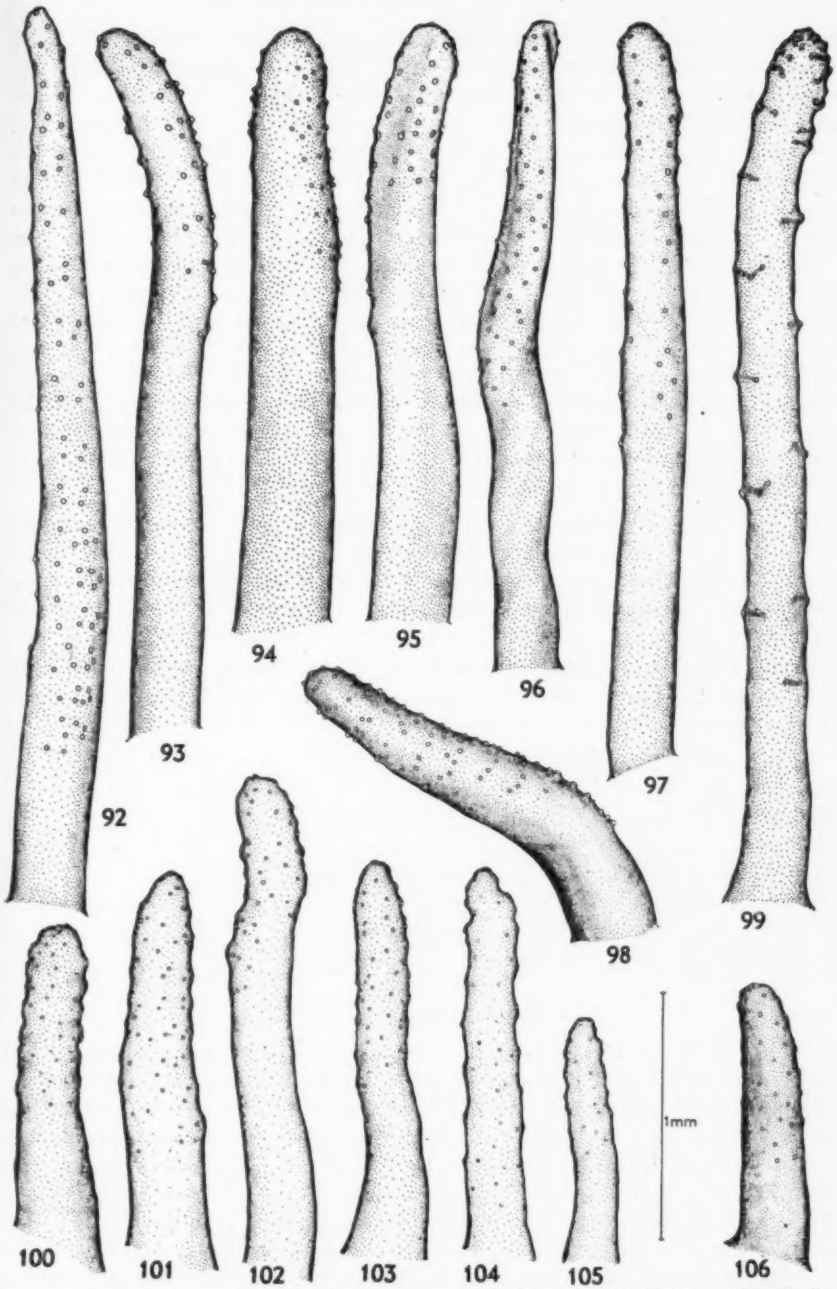
Puparium : Length, 9 mm. ; breadth 3 mm. Long, narrow, not noticeably inflated, except for strongly inflated first abdominal segment ; cuticle pale brownish, pubescence not darkened ; pupal spiracles dark, 2·5–3 mm. long, straight with slightly curved and flattened tips ; spiracular openings in widely separated groups except at tip (Fig. 99).

Taxonomic notes : This species is the smallest of the British *Helophilus* and is at once distinguished by the prothoracic spiracles, which are long and slender, and dark brown ; the other species have pale and short spiracles.

Biological notes : The larvae of this species overwinter and pupate in the spring, there is a summer brood which produces adults in the late summer and these produce the overwintering larvae. The adults have been observed laying eggs in the spaces left by partial decay of *Typha* leaves. The larvae live in ponds containing a large amount of decaying vegetation, particularly where there is *Typha*. The first instar larvae are without dilated tracheal trunks, the trunks being no wider than the trachea in the breathing tube, and only a very faint undulation is present. The puparium is formed with the first abdominal segment of the larval cuticle more strongly inflated than the rest. This is to accommodate the developing head, necessary as the puparium is small and the adult head is relatively large.

MALLOTA CIMBICIFORMIS Fallen

Third instar larva : Length, 25+25 mm. ; breadth, 6 mm. Eristaline shape but more flattened and with pronounced lateral ridge ; three pairs of prominent, narrow, lappets laterally on seventh abdominal segment. Cuticle whitish ;



Figs. 92–106—Pupal spiracles of : (92) *Eristalis pertinax* Scop., (93) *Eristalis sepulchralis* L., (94) *Eristalis intricarius* L., (95) *Eristalis nemorum* L., (96) *Eristalis abusivus* Collin, (97) *Eristalis arbustorum* L., (98) *Eristalis tenax* L., (99) *Helophilus lineatus* F., (100) *Helophilus pendulus* L., (101) *Helophilus hybridus* Loew, (102) *Helophilus frutetorum* F., (103) *Helophilus versicolor* F., (104) *Helophilus lunulatus* Meig., (105) *Helophilus transfugus* L., (106) *Myiatropa florea* L.

pubescence absent on the abdomen from the second segment posteriorly, except for an occasional odd spinule along the ventro-lateral line ; very sparse anteriorly except on the anterior face of the prothorax which has numerous weakly sclerotized, slightly curved spinules the pubescence spinules are mostly branched. Chaetotaxy as *Eristalis sepulchralis* but with AL1 moved postero-ventrally to lie in the same line as AL2 and AL3 and posterior to them ; VL pair very close on thorax and fused on abdomen ; papillae elongate ; lappets on A7 are projections of the cuticle bearing the papillae of L2, L3 and L1 respectively ; setae long and fine, 10–15 around each sensillum. Prolegs elongate and slender, crochets extending outwards over their ends ; about nine primary crochets long and slender with sclerotized tips, secondaries shorter and strongly curved with distal third sclerotized, and smaller accessories ; outer crochets on prolegs of A6 partially anteriorly directed. Anterior spiracle yellow brown ; elongate, stout, with pointed slightly recurved tip ; bearing 25 facets (Fig. 85). Posterior spiracle of Eristaline type with slightly raised slits, pale brown, terminal setae double, one slightly longer than the other. Anal papillae with 12 terminations (Coe, 1953b), formula probably 1 : 1 : 2 : 2.

Puparium : Length, 18 mm. ; breadth, 6 mm. Strongly inflated especially about the middle and slightly compressed so that it is just deeper than wide, tapering equally towards narrowly rounded ends ; brownish ; semi-transparent ; spiracles yellow brown, 4 mm. long, straight with facets on distal two thirds.

Taxonomic notes : There is not likely to be any confusion about the identity of this larva since its pubescence and the form of the sensilla are characteristic.

Biological notes : The larvae live in rot holes of various trees, e.g. elm, horse chestnut, usually at a considerable height above ground so that they are seldom encountered. According to Coe (1953 b) the larval stage probably takes two years, overwintering as a larval stage. Puparium formation occurs in the drier detritus at the top of the rot holes (Coe, 1953 b).

The prothoracic spiracles of this larva are large, stout, and pointed, it is interesting to speculate that they might be used in a manner similar to the hooked spines of *Xylota nemorum* and *Criorhina berberina*.

MYIATROPA FLOREA Linnaeus

Third instar larva : Length, 22+15 mm. ; breadth, 5 mm. Shape typical Eristaline, thorax slightly tapering anteriorly toward truncate anterior end. Cuticle whitish ; pubescence well developed on raised folds, shorter and tending to become absent in furrows ; longer along the lateral lines and minute ventrally ; well developed vestiture of small spinules along the basal segment of the breathing tube ; spinules on anterior prothorax slightly sclerotized, moderately stout and hooked. Chaetotaxy as *Eristalis sepulchralis* with setae little longer than pubescence and on small distinct papillae. Prolegs large ; abdominal prolegs with two well defined semi-circular rows of stout crochets, of which the distal two-thirds is heavily sclerotized ; seven or eight primary crochets but often fewer on the anterior abdominal prolegs, and few minute

accessories ; mesothoracic proleg with usually eight primaries and several rows of accessory crochets. Anterior spiracle pale yellowish, tip rounded and slightly curved backwards with about 14 facets ; the base of the spiracle with some vertical striation (Fig. 84). Posterior spiracles of the eristaline type, dark ; with eight simple long plumose setae. Anal papillae with long unbranched tubes formula 1 : 1 : 3 : 2 (Fig. 20).

Puparium : Length, 14 mm. ; breadth, 6 mm. Laterally inflated, widest on the second abdominal segment ; tapering gradually posteriorly and rapidly anteriorly, anterior end rounded. Grey brown with darker blotches, opaque ; heavy deposition of calcium carbonate on inside. Pupal spiracles small, 1 mm. long, dark brown with black reticulate pattern (Fig. 106).

Taxonomic notes : The larva might be confused with *Eristalis tenax* on account of the crochets, but it differs markedly in the colour of the prothoracic spiracles and in the anal papillae. Fixed larvae often are notably constricted about the anterior end and living larvae will often similarly constrict themselves. The habitat is a very good hint as to the identity of this larva. *Mallota cimbiciformis* which is also found in rot holes has a very distinct appearance.

Biological notes : The larvae are to be found in rot holes and leaf-filled water pockets of various trees, especially beech, and occasionally in wooden water butts which have an accumulation of decaying leaves in the bottom. Coe (1953 a) quotes a note by F. W. Edwards on specimens in the British Museum (Natural History) that some full grown larvae found in a water butt had a tail length of eleven inches. This is probably exceptional though in rot holes a length of up to eight inches is frequently found. Pupation takes place well above the water level, normally with the puparium partially buried ; although, where they have been breeding in the bottom of a water butt, puparia have been found stuck to the sides of the butt with no cover at all. *Myiatropa florea* overwinters as the larva, the adults first appear in the late spring and can be found throughout the summer months till October. A new generation of larvae starts to appear during the summer, which under favourable conditions may produce adults later the same summer. These in turn produce a second generation of larvae which overwinter together with those of the first generation which failed to mature that year.

VOLUCELLINI

Represented by the single genus *Volucella*.

KEY TO THE SPECIES OF *VOLUCELLA*

1.	Body without long papillae posteriorly. With mesothoracic prolegs ; crochets on all prolegs in a single row.....	*V. inanis* (p. 568).
—.	Body with at least six long papillae posteriorly. Without mesothoracic prolegs ; crochets in two distinct rows.....	2.
2.	Dorso-lateral papillae short, much shorter than the six posterior papillae ; a single pair of small papillae near the mid-dorsal line on each abdominal segment	*V. bombylans*.

—. Dorso-lateral papillae long, not distinct from the posterior papillae ; two pairs of small papillae near the mid-dorsal line on each abdominal segment (each papilla is in the D1 position) ..... 3.
3. Maximum length 20 mm. ..... *V. pellucens* (p. 566).
—. Maximum length 30 mm. ..... *V. zonaria*.
The larva of *V. inflata* has not been described.

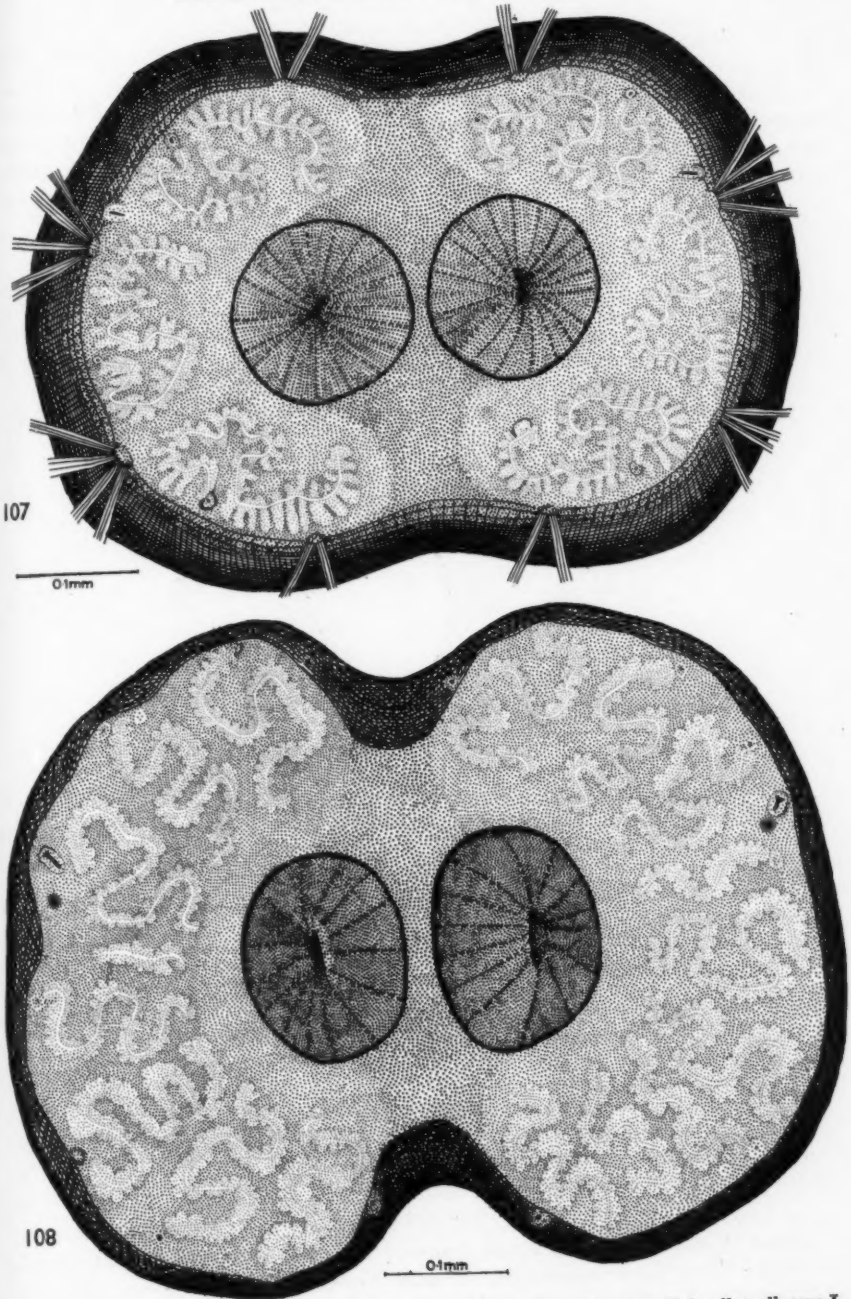
VOLUCELLA PELLUCENS Linnaeus

Third instar larva : Length, 20 mm. ; breadth, 6 mm. Rounded posteriorly, tapering from second abdominal segment forward to the narrow, bluntly pointed, prothorax ; dorsal surface almost flat with four transverse corrugations on each abdominal segment, sides slightly rounded, dorso-lateral line sharply angled ; two elongate conical fleshy papillae dorso-laterally on either side of each abdominal segment, the posterior papillae bear the D4 sensilla ; the anterior papillae are without sensilla as are also a pair of dorsal papillae on the first ridge of each of the second to seventh abdominal segments ; laterally there are similar but much smaller papillae bearing the lateral sensilla ; the dorso-lateral papillae continue on to the eighth abdominal segment and circle the posterior end. Cuticle opaque, yellowish white ; pubescence well developed, short ; some stouter, sclerotized, hooked spinules on prothorax. Chaetotaxy as shown in Fig. 7, the positions of the false papillae are also shown ; two setae to each sensillum. Prolegs well developed on abdomen, absent on thorax ; crochets long and slender, heavily sclerotized ; three or four primaries and four or five secondaries only. Anterior spiracles short cylindrical, disc oblique, sloping down posteriorly ; numerous facets on upper part of perimeter. Posterior spiracles large and squat (Fig. 107), sessile, dorsally on eighth abdominal segment. Anal papillae not developed.

Puparium : Length, 11 mm. ; breadth, 5 mm. Very little difference in shape from the larva, dorsal surface inflated anteriorly, and generally arched dorsally. Pupal spiracles as Fig. 110.

Taxonomic notes : The general appearance and habitat of these larvae render them unlikely to be confused with any other larvae. *V. inanis* is distinct in having a larva without long papillae and possessing mesothoracic prolegs. The larva of *V. pellucens* is very like but smaller than the larva of *V. zonaria*. According to Lundbeck (1916), *V. bombylans* has only three dorsal corrugations per segment while *V. pellucens* has four, the latter also has extra (blind) papillae, and so does *V. zonaria ;* whereas *V. bombylans* has only the usual number which all bear sensilla.

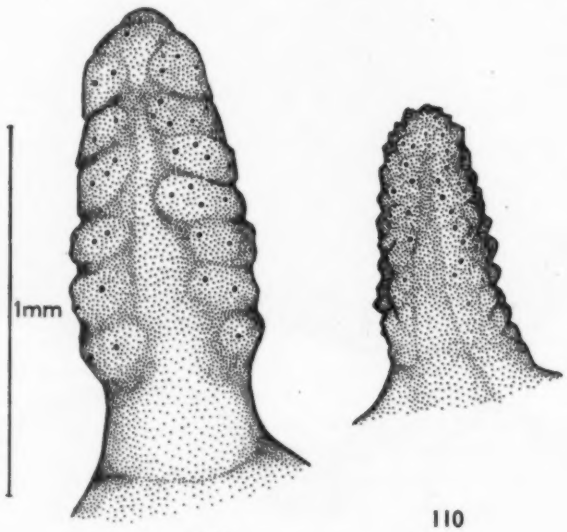
Biological notes : The larvae live as scavengers in the nests of Vespidae and *Bombus*. The larvae spend most of their life in the detritus at the bottom of the nest and only after the hosts have died in the autumn do they scavenge amongst the comb. The larvae complete their growth shortly afterwards and hibernate in the soil until the spring when they pupate near the surface. The eggs are laid on the side of the nest.



Figs. 107–108—Disc of posterior spiracles of third instar larvae of : (107) *Volucella pellucens* L., (108) *Volucella inanis* L.

VOLUCELLA INANIS Linnaeus

Third instar larva (based on the puparium): Length, 22 mm.; breadth, 6 mm. Shape as *V. pellucens*, without elongate papillae; apparently only three corrugations dorsally on each abdominal segment (Künckel d'Herculais, 1875); no false papillae. Pubescence well developed, short; few small stout hooks



109 110

Figs. 109–110—Pupal spiracles of: (109) *Volucella inanis* L., (110) *Volucella pellucens* L.

on prothorax. Chaetotaxy as shown (Fig. 6); papillae small. Prolegs present on first six abdominal segments and on mesothorax; crochets in a single row of eight or nine, very long and heavily sclerotized. Anterior spiracle short and stout as *V. pellucens*. Posterior spiracles longer than wide, terminal and sessile, disc as Fig. 108.

Puparium: Length, 13 mm.; breadth, 6 mm. Shape as *V. pellucens*, brownish. Pupal spiracles as Fig. 109.

Notes: See *V. pellucens*.

MICRODONTINI

Only one species available.

MICRODON EGGERI Mik

Third instar larva: Length, 9 mm.; breadth, 5 mm. Almost hemispherical; body from metathorax to posterior end strongly convex and with broad elliptical outline; ventral side flattened; mouth parts, pro- and mesothorax very reduced, placed ventrally under metathorax where they lie flat

with the ventral surface ; without the creases or corrugations normally found on the surface of Syrphid larvae (Fig. 111). Cuticle opaque whitish with pattern of brown tubercles bearing tufts of brown spinules (Fig. 112) ; well developed fringe of large bifid spinules (Fig. 113) laterally on the margin, with band of smaller tufted spinules dorsally ; ventral pubescence well developed,

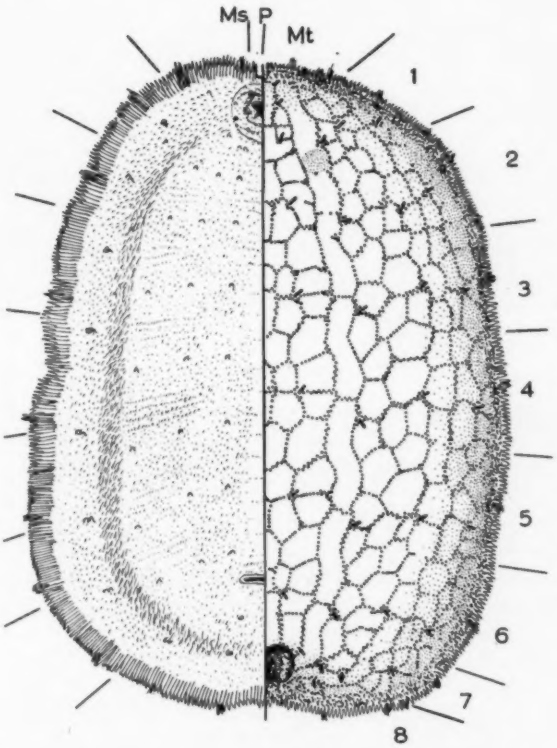
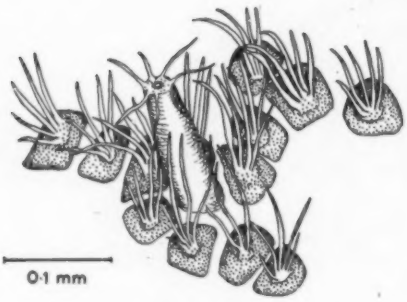


Fig. 111—*Microdon eggeri* Mik, third instar larva, longitudinal right halves, dorsal to the right ventral to the left. P, prothorax ; Ms, mesothorax ; Mt, metathorax ; 1–8, abdominal segments The segmentation can be distinguished by the lines of segmental sensilla and repetitive pattern of the pubescence.

fine, with ventro-lateral band of longer spinules. Chaetotaxy* arrangement as shown in Fig. 111 ; ventral papillae short conical with vestigial setae ; dorsal papillae long cylindrical with some short radial setae at the tip (D1, 2, 4, L1) ; lateral papillae fairly long with several long seta (L2 or L3) (Fig. 113). Prolegs

* The chaetotaxy has not been completely solved for the pro- and mesothorax ; nor for the lateral abdominal sensilla, as only two of the three laterals have been found. The marginal lateral (L2 or L3) shows signs of being double as there appear to be two canals in the papilla ; these are not visible in those of the metathorax, and the anterior one of the eighth abdominal segment, which should in fact be single. It may be possible to confirm this with a first instar larva.

and crochets absent. Functional prothoracic spiracles absent. Posterior spiracles (Fig. 114) sessile ; sides covered with dense scale-like excrescence which is longer and overhanging at the base of the spiracle ; disc slightly curved, spiracular openings broken up into numerous small oval apertures ; plumose setae absent, four pairs of single setae arranged on the disc as shown.



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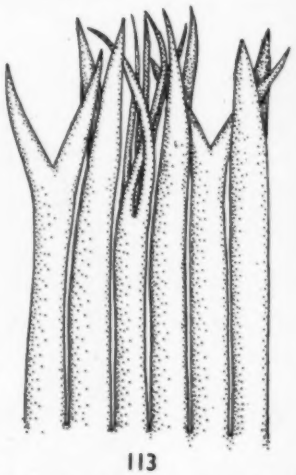

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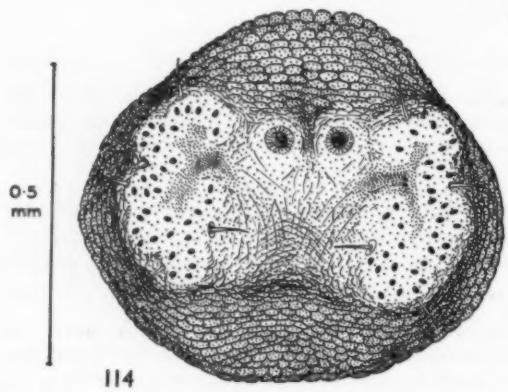
Figs. 112–113—*Microdon eggeri* Mik, third instar larva, sensillum and pubescence ; (112) dorsal, (113) lateral.

Puparium : Differs from larva only by being attached by the ventral side and having the pupal spiracles, which are short, conical, dark brown, and have some longitudinal sculpturing ; the openings are all single and grouped on the rounded end of the spiracle (Fig. 115).



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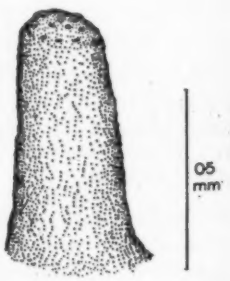

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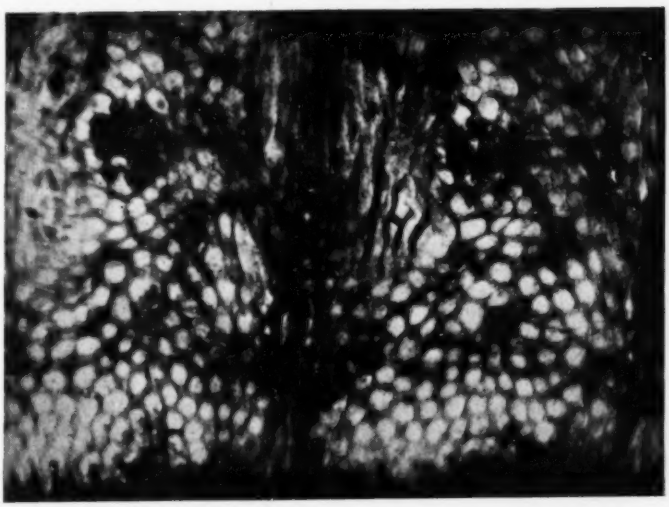
Figs. 114–115—*Microdon eggeri* Mik, spiracles ; (114) third instar, disc of posterior spiracles, (115) pupal spiracle.



Figs. 116–117—Photographs of the third instar cuticle after puparium formation of : (116) *Chrysogaster metallina* F., (117) *Chrysogaster splendida* Meig.

Taxonomic notes : Greene (1956) has produced a key to the larvae of 18 American and Australian species using the reticulate pattern of tubercles, the marginal pubescence, the posterior spiracles, and the general shape as characters. Syms (1935) states that *M. mutabilis* has the reticulate pattern of tubercles confined to the sides, the mid-dorsal surface being smooth, but he does not give the source of this information.

Biological notes : The biology of *M. mutabilis* is discussed by Donisthorpe (1927) and *M. eggeri* by Syms (1935) ; the larvae of both species have been proved by these authors to feed on the solid pellets ejected from the hypopharyngeal pockets of ants in whose nests they live. The life cycle takes one year, the larvae pupate in the spring and the adults emerge about one month later, eggs are laid in the early summer and the larvae hatch in about eight days. The hosts are ants, usually of the sub-family Formicinae.

ACKNOWLEDGMENTS

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THE REPRODUCTIVE SYSTEM OF THE AMPHIBIOUS SNAIL *SUCCINEA PFEIFFERI* ROSSMASSLER

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[Accepted 13th December 1960]

(With 2 figures in the text)

Following a brief histological examination, the genital system of *Succinea pfeifferi* was found to correspond with the pulmonate pattern and similarities were found with members of the Basommatophora and with *Helix*, a more specialised stylommatophoran.

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INTRODUCTION

Succinea pfeifferi is a stylommatophoran pulmonate belonging to the family Succineidae and is of common occurrence in moist habitats in England. Thus, it is usually found on vegetation in marshes and beside rivers, canals and ponds. The amphibious Succineidae are among the primitive members of the Stylommatophora and this paper is one of a series of publications on the genital systems of the pulmonate gastropods, (Duncan, 1958, 1959, 1960 a and b). Although Quick (1933, 1936, 1939 a and b) and Pilsbry (1948) have made studies of the gross morphology of a variety of species of *Succinea*, little account of the histology of the component organs has been found. A brief histological examination of the genital system of *Succinea pfeifferi* was therefore made, using similar staining techniques to those employed previously, when studying the reproductive organs of the Basommatophora, and a description is given below. In this way, it was hoped to evaluate the relationships of *Succinea*, as seen by a study of the genital system, with members of the Basommatophora and with the more specialised members of the Stylommatophora, (Duncan, 1960 a). The plan of the component organs of the hermaphrodite genital system of *Succinea* is shown in Fig. 1.

MATERIAL AND METHODS

Specimens of *S. pfeifferi* were collected from the vegetation at Lewes Brooks, Sussex and dissected in the laboratory in a saline medium isotonic with

the blood of *Lymnaea stagnalis*, and the gross morphology was studied. For histological work, the dissected snails were fixed in Susa and sectioned at 8μ, the sections being stained in Heidenhains azan or iron haematoxylin.

OVOTESTIS AND HERMAPHRODITE DUCT

Hanna (1940) notes that, in *Succinea chrysis*, the testis forms the extreme end of the hermaphrodite organ and in this species is usually distinct from the ovary. However, in its histological structure, the ovotestis of *S. pfeifferi*

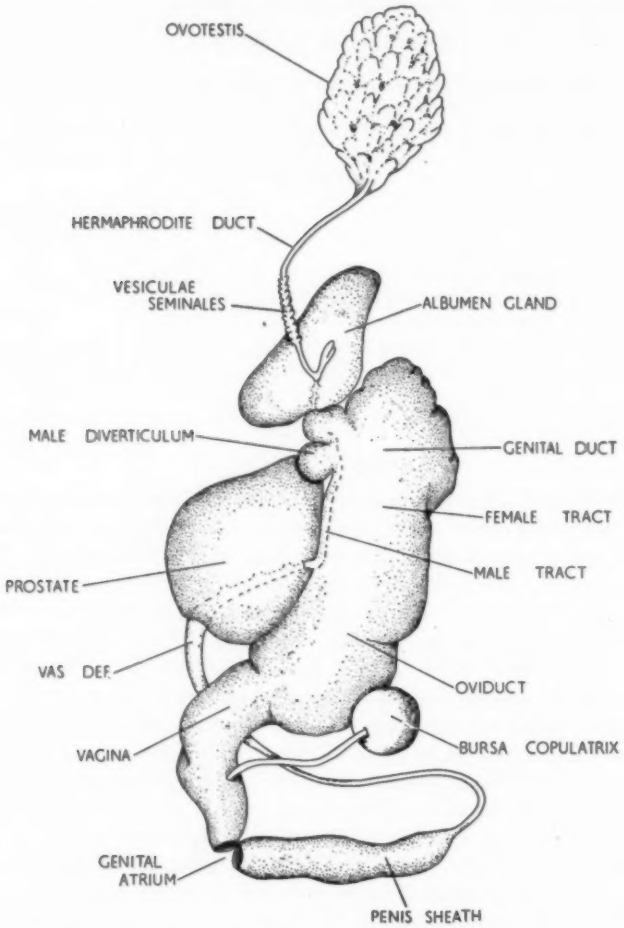

Fig. 1—Dorsal view of the dissected reproductive organs of *S. pfeifferi*.

closely resembles the characteristic condition described in members of the freshwater Basommatophora (Archie, 1942, ; Duncan, 1958). The male and female gametes develop in the same follicle, the ova remaining attached to

the wall of the gonad until mature, while the spermatozoa fall into the lumen and continue their development there.

The epithelium of the hermaphrodite duct is formed of ciliated, cuboidal cells and has an investing connective tissue sheath which is surrounded by a layer of black pigment. After staining with azan, the cytoplasm of the epithelial cells appears blue and the cilia yellow, as in members of the Hygrophila. The " seminal vesicles " consist of a single pair of diverticula, fused together at their bases and separate only at their free ends, being covered with pigment and enclosed in a common connective tissue and muscle complex. Composed of columnar cells with basal nuclei, they open into the hermaphrodite duct immediately before its entry into the albumen gland.

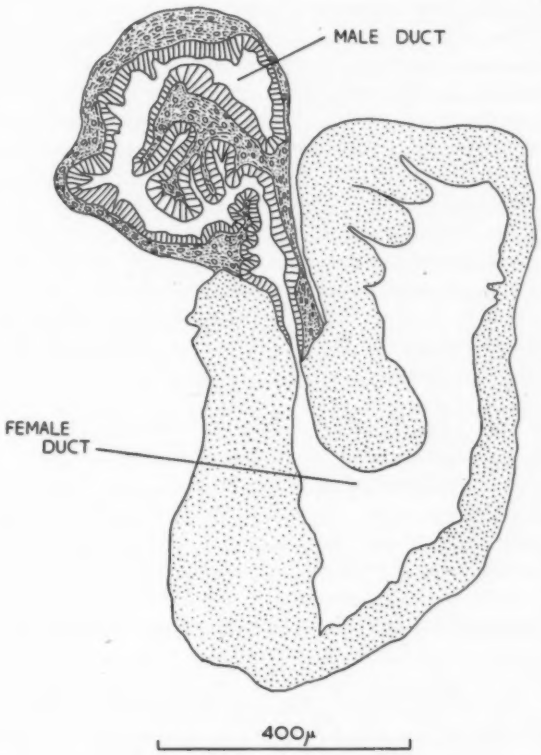

Fig. 2—Diagrammatic transverse section of the common genital duct.

ALBUMEN GLAND AND GENITAL DUCT

The structure of the albumen gland is identical with that described in the Hygrophila (Duncan, 1958, 1960 b), being composed of follicles, each with its own small lumen and lined by secretory cells. These have a large, basal nucleus and after staining with azan are packed with blue-staining secretory

globules. The central lumen of the gland is completely lined by a ciliated epithelium and runs the length of the longitudinal axis of the organ.

There is a gradual transition from the histological structure of the epithelium lining the lumen of the albumen gland into that of the common genital duct, whose epithelium is convoluted and consists of columnar, ciliated cells, outside which are packed loose, vesicular cells, forming an extensive connective tissue sheath. In mature snails, however, this genital duct almost immediately becomes incompletely separated into male and female sections. These are histologically distinct portions of a common tract and, apart from a narrow inter-communicating channel, the two systems are functionally separate entities. The male tract is also composed of ciliated, columnar cells and has a small, highly convoluted diverticulum of similar histological structure (Fig. 1). The female portion of the common genital duct is composed of the typical, oviducal, glandular cells which seem to be a feature of the pulmonate oviduct, although, in *Succinea*, there is a general accent on histological simplicity. Thus, throughout its length only one type of secretory cell is found. It is simple and columnar, with a basal nucleus and vacuolated cytoplasm which stains pale blue with azan. Tetrahedral, ciliated cells are wedged between the apices of these glandular cells. When separated from the male system, the female duct is a simple, distended tube, although somewhat twisted, and throughout its length there is no apparent differentiation into distinct regions. The vas deferens becomes separated about one-third of the way along the female duct, but a small tract of the ciliated cells continues along the length of the oviduct, joining the ciliated epithelium of the vagina. Apart from this, tracts of cuboidal, ciliated cells are absent and the whole system appears remarkedly uniform.

VAGINA AND BURSA COPULATRIX

The wall of the vagina is formed of columnar, ciliated cells and is thrown into corrugations and invested in a connective tissue and muscle sheath. The female orifice opens to the exterior at the genital atrium on the right-hand side of the head. The bursa copulatrix of the pulmonates exhibits little variation and no deviation from the standard pattern is found in *Succinea*. It is relatively large and the glandular, columnar cells are characteristically non-ciliated, although its duct, surrounded by a muscle sheath, has a fine ciliation.

PROSTATE GLAND, VAS DEFERENS AND PENIS

The prostate gland is a spheroidal organ containing an intricate series of follicles which are enclosed within a very thin sheath, reminiscent of the condition in the Planorbidae (Duncan, 1960 b). Similarly, the histology of the prostate corresponds with that described in the Physidae, Planorbidae and Ancylidae and differs from the condition in the Lymnaeidae. Thus, each follicle has a central lumen surrounded by glandular cells, which have a large, basal nucleus. Above the nucleus, the cytoplasm, which stains blue with azan when mature, becomes packed with secretory globules. The follicles unite into collecting ducts which join the male duct. The latter separates

from the common genital duct and passes into the body of the prostate (Fig. 1). It re-emerges on the opposite face as the vas deferens. This is ciliated throughout its length and the cuboidal cells of which the wall is composed are soon replaced by a columnar, corrugated epithelium. There is an extensive muscle sheath. Eventually, the vas deferens becomes very convoluted and enclosed within the muscular tube of the penis.

DISCUSSION

The general pattern of organisation of the pulmonate genital system is immediately apparent in *Succinea pfeifferi* and this is emphasised by a study of the component organs. Histologically, the ovotestis, hermaphrodite duct, albumen gland and the bursa copulatrix resemble the corresponding organs described in members of the Basommatophora and in a more specialised stylommatophoran, *Helix*. In the Hygrophila the female tract is completely separated from the male duct and several distinct regions are recognisable. As Holm (1949), working on *Lymnaea stagnalis* has pointed out, the glandular cells found throughout the female duct are fundamentally the same, there being a variation from the basic pattern in the different regions. These secretory cells are columnar, give a characteristic staining reaction with azan at the different phases of glandular activity, and have small, ciliated cells wedged between their apices. In both *Succinea* and *Helix* the female tract is essentially simple ; there is no division into separate regions and the characteristic secretory cells are found throughout.

Hubendick (1947) has shown that two different types of prostate are found in the Hygrophila. In the Lymnaeidae the surface enlargement is achieved by the widening of the vas deferens and, with certain exceptions, by the development of inwardly directed folds in its walls. In the Physidae, Planorbidae and Ancylidae the prostatic follicles are formed by evaginations which develop in an outward direction and are undoubtedly homologous in these three families. The two types of prostate are markedly different in histology and staining reaction (Duncan, 1960 a and b), and the prostate gland of *Succinea* is formed of follicles which correspond histologically to the second type.

In *Chilina robustior* (Chilinidae, Basommatophora) the glandular portion of the common genital duct is structurally hermaphrodite, although subdivided into male and female tracts. The female portion is supplied with well-developed mucous glands and the male groove is lined by an extensive prostatic epithelium which also resembles that found in *Succinea*. It has therefore been suggested that the genital system of *Chilina* might closely resemble the ancestral condition of the Stylommatophora, (Duncan, 1960 a).

Other workers on the Succineidae (Quick, 1933, 1936) have described a pair of seminal vesicles opening into the hermaphrodite duct close to the point where it enters the albumen gland. From their histology, they appear to be identical with the fertilisation pockets found close to the albumen gland in the higher Basommatophora and they are probably homologous with the fertilisation sacs or pockets found throughout the Pulmonata.

ACKNOWLEDGMENTS

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SEASONAL CHANGES IN THE DISTRIBUTION OF THE TESTIS LIPIDS OF THE CASPIAN TERRAPIN *CLEMMYS CASPICA*

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(With 2 plates and 3 figures in the text)

The testis of *Clemmys caspica* undergoes a sequence of well defined cyclical events. These include a seasonal enlargement of the Sertoli cells and the genesis of large quantities of lipoidal material in their cytoplasm. Intra-tubular lipids disappear at the onset of the following spermatogenetic rhythm. This seasonal accumulation of dense sudanophil material within the seminiferous tubules and its disappearance prior to spermatogenesis is comparable with the events which occur in seasonal birds and other sub-mammalian vertebrates. A lipid cycle occurs also in the interstitial Leydig cells which become denuded of their lipid contents at a time when spermatozoa are being discharged from the epididymal canals. This is the time of maximum sexual activity.

By September the seminiferous tubules have reached a peak of spermatogenesis and contain bunched spermatozoa. This is then followed by the transference of spermatozoa from the tubule lumena into the epididymal canals where they are stored for several months until the following breeding season. Meantime the 'spent' tubules become collapsed and enter a period of sexual negativity. In this, the terrapin differs from the viper (*vipera berus*) where the next spermatogenetic rhythm begins almost immediately after the spring shedding of spermatozoa and becomes well-established whilst the tubules are still clotted with large quantities of post-nuptial lipids.

The spermatogenetic cycle closely parallels the environmental temperature cycle. It commences in April when environmental temperatures are rising rapidly and does not start to decline until October, by which time the daily temperature is beginning to drop. This cycle commences whilst day-lengths are increasing, but declining day-lengths after the summer solstice (21st June) appears to have no effect on spermatogenesis which continues unabated until late September.

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INTRODUCTION

There appears to be a pattern of cyclical events in the male gonad which is common to a number of sub-mammalian vertebrates. In birds, for example, as the seasonal spermatogenesis and sexual behaviour reaches its peak, there is an accompanying progressive discharge of cholesterol-positive lipids from the interstitial Leydig cells of the testis, so that by the time the adjacent seminiferous tubules have filled with spermatozoa, the Leydig cytoplasm has become denuded of lipids and cholesterol. There then follows a post-nuptial regeneration in preparation for the next sexual season (Marshall, 1949, 1955). Cyclical changes also occur in the tubules. After spermatozoa have been shed there is a profound metamorphosis involving the genesis of large quantities of lipoidal material and profuse cholesterol.

Such a complete post-nuptial tubule metamorphosis does not occur in seasonal mammals (Lofts, 1960) although an interstitial cycle is still retained, but it is a regular part of the cycle of certain teleost fishes (Marshall & Lofts, 1956 ; Lofts & Marshall, 1957) and occurs in at least one amphibian (Lofts & Boswell, 1960). The function of this seasonally recurring reservoir of tubule lipid and cholesterol is not known, but recently Lofts & Marshall (1959) have demonstrated that, in birds at least, it may be of endocrine significance.

Although there exists an extensive literature dealing with the reproductive cycles of various members of the Reptilia, the majority of workers used traditional wax-embedding techniques which result in the dissolution of cytoplasmic and other lipids. Thus, many aspects of the testis cycle escaped notice until comparatively recent times (Altland, 1951 ; Marshall & Wolf, 1957). In *Vipera berus* the testis is now known to undergo cyclical changes in the lipid distribution which, although differing in some aspects, closely parallels the avian pattern (Marshall & Wolf, 1957).

The aims of the present study were threefold :

(1) To determine whether in the seminiferous and endocrine elements of the testis of a chelonian reptile there occur events comparable with those in birds and other sub-mammalian vertebrates :

(2) to compare the testicular changes of this ancient group with more ' modern ' reptiles, such as the viper ;

(3) to correlate, as far as possible, observed events in the breeding cycle with external environmental fluctuations in photoperiodicity, temperature and rainfall.

MATERIALS AND METHODS

The Caspian terrapin, *Clemmys caspica*, is a common species in Asia Minor and occurs in many areas around the Caspian Sea. The specimens used in the present investigation were collected in Iraq at Gurmah, near Fallujah, some 50 miles west of Baghdad. In this locality there is a small, stagnant lake with an area of seven to ten acres. Clumps of *Phragmites* grow in abundance around its shores and the roots form a major part of the terrapins' diet. There is also an irrigation canal with fairly fast flowing water which draws its supply from the Euphrates near Fallujah.

The animals were collected either from the lake or the canal and would sometimes be surprised basking on the banks. Males were found to be considerably more agile than the females. The present study is based on some fifty-three terrapins which were collected from this locality throughout the year. Occasionally visits were delayed by the impassability of the roads, but with the exception of July, specimens were obtained in every month of the year.

As soon as the collecting expedition returned to Baghdad, the animals were weighed, killed and the gonads dissected out. After measurement of the whole organ the material was subjected to the following uniform procedures. 1. One testis was fixed in Bouin's fluid and subsequently wax embedded. This was sectioned at a thickness of 6μ and stained with iron haematoxylin and orange G for examination of the spermatogenetic condition. 2. The remaining testis was placed in formal-calcium and gelatine embedded. Gelatine sections 8μ thick were coloured with Sudan IV or Sudan black to reveal the lipids, and counterstained with haemalum. 3. Smears of the fresh epididymis were made and examined for sperm motility.

Some female specimens were also collected and after dissection the ovary and oviduct were immersed whole in the above mentioned fixatives.

RESULTS

Seasonal histological changes in the testis

January. The seminiferous tubules average 150μ in diameter and contain a few inactive spermatogonia. Occasional tubules possess one or two isolated primary spermatocytes, but all other spermatogenetic stages are absent (Pl. 1, fig. 1). There is a complete peripheral ring of elongated Sertoli cells and the majority of tubule-lumina are empty, although a few still retain some necrotic nuclei and debris. The Sertoli cytoplasm contains numerous large lipoidal droplets (Pl. 1, fig. 2). The interstitial tissue is extensive and contains a profusion of blood vessels. Leydig cells possess small sudanophil droplets.

Epididymides contain massed spermatozoa and the largest canal measures 450μ in diameter. The epididymal smear revealed active spermatozoa.

February. The testis is little changed from that described above. Tubule diameters average 140μ and the only germ cells present are a few spermatogonia and, in some tubules, occasional persistent spermatozoa. The Sertoli cells still contain profuse cytoplasmic lipids. The interstitial Leydig cells are also lipoidal.

Epididymides are larger and still filled with a dense mass of motile spermatozoa. Canal size has increased to 600μ.

March. Tubules are 110μ in diameter and show no increase in spermatogenetic activity. The Sertoli cell condition, too, appears unchanged from that observed in the preceding month. There has been a proliferation of new cells in the interstitial tissue and a few cell mitoses are seen during this period. The juvenile cells are non-lipoidal but adult Leydig cells are still filled with dense lipid droplets.

Active spermatozoa persist in the epididymal canals which remain 600μ in diameter.

April. There is a recrudescence of spermatogenesis during this month. Spermatogonia have become more numerous and are undergoing active cell division. This has led to a slight increase in tubule diameter to 140μ. Sertoli cells have increased in size and their cytoplasm now completely occludes the tubule lumen. Intra-tubular lipid is still profuse (Pl. 1, figs. 3 and 4). Some mitotic divisions are still seen in the interstitium and cells are very numerous. Adult Leydig cells still contain dense cytoplasmic lipid.

Epididymal canals are 500μ diameter with dense masses of spermatozoa (Pl. 2, fig. 3). The smears still reveal active spermatozoa.

May. Tubules have increased to 160μ diameter and contain numerous spermatogonia, primary and secondary spermatocytes. Spermatids have been produced in some tubules. The lumina are filled with the ripening germinal cells and the Sertoli cells are compressed. Their cytoplasmic lipid has largely disappeared. The interstitial Leydig cells have also become denuded of their lipids and now contain relatively few sudanophil droplets (Pl. 2, fig. 1).

The spermatozoa in the epididymal canals (500μ diameter) appear less dense.

June. Tubules have reached a diameter of 175μ. All stages of spermatogenesis are now represented though spermatozoa have not yet appeared in large numbers. Both Sertoli and interstitial cells are without cytoplasmic lipids (Pl. 2, fig. 2).

Epididymides contain fewer spermatozoa but the canals are still 500μ in diameter and active sperm are still present in the smears.

July. No specimens were collected during this month.

August. Tubules have now attained their maximum size and are 450μ in diameter. Within, all spermatogenetic stages are common, including bunched spermatozoa. Sertoli cells are compressed by the ripening germ cells and devoid of any cytoplasmic sudanophil droplets. Within the interstitium the new generation of Leydig cells are enlarging and becoming compressed by the expanding seminiferous tubules. No interstitial lipids are present.

Epididymides are without spermatozoa and the canal lumen is now only 300μ diameter (Pl. 2, fig. 4). For the first time, there is an absence of active spermatozoa in the epididymal smears of the majority of specimens though one large terrapin still retained some.

September. Testes collected during this month show little change from that described for August. Tubules are still distended (450μ diameter) and contain bunched spermatozoa. Both Sertoli and Leydig cell cytoplasm are without lipoidal material.

Epididymal canals are still without spermatozoa and show a further reduction to 250μ diameter.

October. There is a decrease in tubule size to 300μ diameter. Spermatogonial multiplication has ceased and there is a gradual maturation of spermatocytes and spermatids into spermatozoa which are now free in the tubule lumen. Sertoli lipid has not yet reappeared, but the interstitial Leydig cells are showing

the first signs of their seasonal accumulation and contain a few small sudanophil droplets in their cytoplasm.

Epididymides are once again increasing in size (canals 600μ) and starting to receive spermatozoa from the seminiferous tubules. The smears contain extremely active spermatozoa.

November. Tubules, 200μ in diameter, contain spermatogonia and spermatozoa only. Other spermatogenetic stages have matured into spermatozoa and are no longer represented (apart from an isolated primary spermatocyte in odd tubules). Some spermatozoa have been discharged leaving empty lumina. Sertoli cells contain a scattering of fine lipoidal droplets. The Leydig cell cytoplasm has increased in lipid content and now display obvious discrete sudanophil droplets.

Epididymides contain sperm-filled canals 600μ in diameter. Active spermatozoa are seen in the smears.

December. Sperm discharge has continued and tubule size has shrunk to 150μ diameter. Many tubules are now cleared of spermatozoa but others still retain a mass in the lumen. Peripheral spermatogonia are the only other germ cells present. Sertoli cells are once again enlarging and have acquired much cytoplasmic lipid. Leydig cells, too, contain numerous sudanophil droplets.

Dense masses of active spermatozoa are present in the epididymal canals which are now 750μ wide.

Seasonal variation in the ovary and oviduct

As in the male, the reproductive organs of the female also undergo considerable seasonal variation in size. Fig. 1 demonstrates the seasonal fluctuation in the diameters of the largest follicle and oviduct respectively. From this, it is seen that follicle enlargement occurs throughout March and April. Minimum size is in December and January. Ovulation takes place during April and May and some specimens collected during this period had eggs in the oviducts. The enlargement of the oviduct closely parallels that of the ovary.

When the variations in the female gonad and accessory organs are compared with the cyclical changes in the male gonad (Fig. 2), ovulation is seen to coincide with the discharge of spermatozoa from the epididymal canals. At this period the seminiferous tubules are without spermatozoa, possessing only juvenile germ cells. During the succeeding months, from May to September, the ovary and accessory organs gradually regress and become quiescent, whereas the testis, on the other hand, undergoes a recrudescence of spermatogenetic activity accompanied by an expansion of the seminiferous tubules. Ovary expansion during February and March coincides with testis shrinkage in male specimens, and maximum ovary size is reached at the same period as minimum testis size.

The sexual cycle and the environment

It is a well-known fact that many reptiles have markedly seasonal patterns of breeding, but the role played by environmental factors in the determination of this periodicity has been studied in only a few species and in no case has it

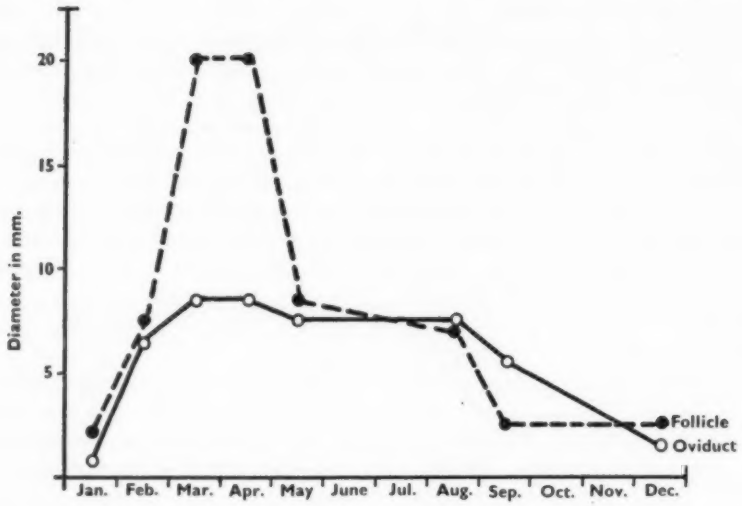

Fig. 1—Seasonal variations in size of the oviduct and follicles of *Clemmys caspica*.

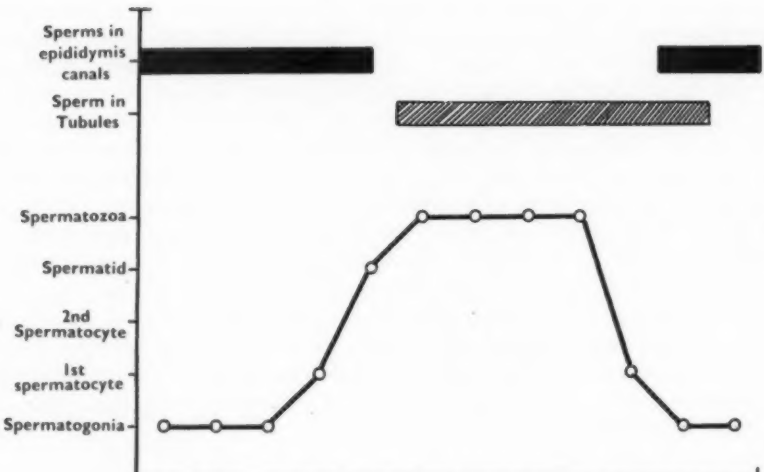

Fig. 2—Seasonal changes in the spermatogenetic condition of the seminiferous tubules of *Clemmys caspica*.

been possible to make an adequate synthesis of physiological and ecological data. In the present study daily records of sunshine, rainfall and temperature were obtained in the hope that a correlation between environmental changes and the internal rhythm of reproduction might be attempted.

Meteorological data was collected over three years and the monthly averages are summarised in Fig. 3.

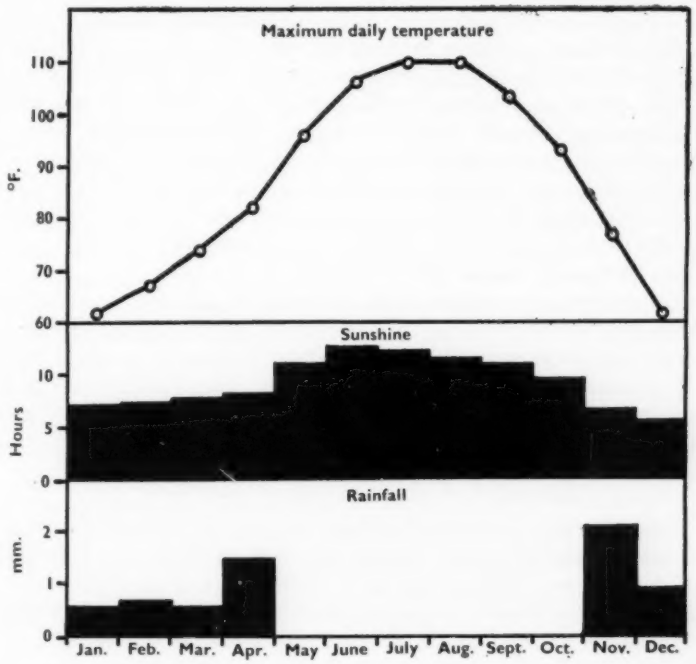

Fig. 3.—Seasonal climatic variations of the environment.

The internal testicular events described above fall into the following well-marked phases :

Phase I, May to September (period of spermatogenesis)

There is a recrudescence of spermatogenetic activity during April which continues throughout the succeeding five months. When it is initiated there is much intra-tubular lipid which rapidly disappears and by the time the first primary spermatocytes are formed the seminiferous elements are without sudanophil material. A new generation of Leydig cells arises in the interstitium but does not yet begin its seasonal accumulation of lipid. The epididymides have discharged their spermatozoa and the canals remain empty for the most of this period.

These events begin while day-length is on the increase and temperature is rapidly rising. The peak of spermatogenetic activity is reached around, or soon after, the summer solstice (21st June) and is maintained during the succeeding two months while day-length is decreasing. The rhythm ceases at a time when temperature starts to fall. Rainfall during this phase is negligible.

Phase II, October to March (period of rehabilitation)

During this phase the testis appears morphologically to become quiescent, decreasing in size to its minimum measurement, and within, showing no spermatogenetic activity. This is, however, as has been shown previously, a period of profound change. Spermatozoa leave the tubules and become stored in the epididymal canals. After their ejection, the tubular elements undergo steatogenesis ; the Sertoli cytoplasm becomes filled with dense lipoidal material and the cells themselves enlarge and eventually completely block the tubule lumen. In the interstitium the Leydig cells slowly begin to accumulate small lipid droplets and are quite heavily lipoidal by the end of the period. The epididymal canals become densely packed with free spermatozoa and assume their maximum size.

These rehabilitative processes begin while day-length and temperature are both decreasing. By December the temperature has fallen to its lowest level and remains so during January and early February. It then begins to rise slowly throughout March. By this time day-length is increasing at the rate of about three minutes per day. Most of the annual rainfall occurs during this period.

Phase III, April (period of reproduction)

This phase overlaps the preceding two. During late March to early May copulation occurs and the spermatozoa are discharged from the epididymal canals which become reduced in size as a result. The Leydig cells show their maximum secretory condition. Sperm shedding is followed by the succeeding spermatogenetic cycle and the rehabilitation of the interstitium.

These culminating events occur at a period of rapidly rising temperature and small daily increases in photoperiod.

DISCUSSION

The cyclical events that occur in the seminiferous tubules of *C. caspica* are almost identical with the post-nuptial tubule metamorphosis of the avian gonad. These involve a rapid genesis of intra-tubular lipid in the discharged seminiferous elements which remains for three to four months and then gradually clears. The last traces of tubule lipids disappear with the main upsurge of the next season's spermatogenesis. This differs from the observed events in *Vipera berus* where the succeeding spermatogenetic rhythm begins almost immediately after the spring shedding of spermatozoa and becomes well-established whilst the tubules are still clotted with large quantities of post-nuptial lipids (Marshall & Wolf, 1957). The latter mechanism also occurs in the pike (Lofts & Marshall, 1957) and it has been suggested that this may be an adaptation related to the poikilothermic condition and the thermal

fluctuations of the environment to which these temporate animals are subjected (Marshall & Wolf, 1957). A three to four months' delay between tubule discharge and the succeeding spermatogenetic rhythm is an inherent part of the internal rhythm of reproduction in the chelonia and occurs in species of northerly latitudes (Herlant, 1933 ; Risley, 1938 ; Altland, 1951) as well as in more arid areas. In the present investigation the thermal fluctuation in the environment is about 50°F between maximum and minimum figures. Here too, however, as in other poikilotherms, spermatogenesis occurs with rising environmental temperatures.

The cycle of the Leydig cells is essentially similar to that of the interstitial cycle in birds and other seasonal vertebrates such as certain fishes (Marshall & Lofts, 1956), the frog (Lofts & Boswell, 1960) and the mole (Lofts, 1960). There occurs a cyclical accumulation and disappearance of sudanophil droplets in their Leydig cell cytoplasm. Where the present species differs from the avian pattern is in the 'timing' of such rhythmical activity, but this can probably be attributed to the mechanism, common to many turtles, of storing spermatozoa in the epididymis. In birds, the Leydig cells start accumulating their cytoplasmic lipids during the post-nuptial period, and by the onset of the following season's spermatogenesis, are heavily impregnated. These cells then rapidly lose their lipids whilst adjacent tubules are reaching their peak of activity. This is considered to be indicative of sex hormone secretion and occurs at a time when sexual behaviour is at its peak (Marshall, 1951). In the turtle, the seminiferous tubules reach their peak of activity and discharge their spermatozoa whilst the adjacent interstitium is relatively immature and only meagrely lipoidal. The maximum secretory appearance occurs just before the spermatozoa are discharged from the *epididymal canals*, and, like the bird, when maximum sexual behaviour occurs. Unlike the bird, however, the tubules at this stage are reaching the end of their period of sexual negativity and spermatogenesis soon begins once more.

Risley (1938), basing his observations on a study of the musk turtle, *Sternotherus odoratus*, has stated that no seasonal changes occur in the interstitial cells, and further, that no seasonally variable secondary sexual characters are known in turtles. The present investigation has demonstrated that some turtles, at least, have a seasonally varying interstitium and a similar sequence has also been reported in the box turtle, *Terrapene carolina* (Altland, 1951). Many lizard species have well-marked secondary sexual features (Pope, 1956) but sexual dimorphism in the chelonia is not very well-marked. However, recently Evans (1951, 1952) has reported that claw size in turtles is influenced by male sex hormones, and castration of box turtles produces a regression of the epididymis (Hansen, 1938).

In the absence of experimental data we cannot fully evaluate the relative importance of temperature and day-length in the control of the events outlined in this investigation. The photoperiodic responses of reptiles are little understood and relatively little literature exists on this subject. Burger (1937) reports that in the turtle *Pseudemys elegans* an artificial increase in day-length will interrupt the spermatogenetic cycle and initiate the start of a new cycle. Clausen & Poris (1937), and Bartholomew (1950, 1953) produced an acceleration

of spermatogenesis by increased photoperiod in *Anolis carolinensis* and *Xantusia vigilis* respectively. In the latter species, the author states that males are more responsive than females and that the rate of photoperiodic response increases directly with increasing temperature. Galgano (1951) has examined the responses of *Lacerta sicula* to various combinations of temperature and photoperiod and has suggested that temperature might control spermatogenesis while photoperiod controls testicular secretions. In *Clemmys* the spermatogenetic cycle has here been demonstrated to follow closely that of the environmental temperature, starting with the sharp rise in April and ceasing when the temperature starts to fall during September. Day-length seems an unlikely stimulus in these events since spermatogenesis still continues even though the photoperiods start to decrease after 21st June. The testis remains quiescent under the increasing day-lengths of January to March. The interstitial cycle follows the photoperiodicity more closely and is generally in agreement with Galgano's hypothesis.

It is interesting to note that the epididymis contains motile and apparently mature spermatozoa for about six months before fertilization occurs (Fig. 2). For the most of this time, however, the female has regressed ovaries. A rapid enlargement and maturation of the follicles occurs during February and March, and is soon followed by fertilization during the succeeding month.

It is of phylogenetic interest that the breeding cycle of this chelonian closely resembles that of the anuran Amphibia. The seasonal changes in *Rana temporaria* have been likened to those of the viper as undergoing a renewal of spermatogenesis immediately after sperm discharge whilst the genesis of intra-tubular lipid is taking place (Marshall & Woolf, 1957). In fact, however, this is the period of so-called pre-spermatogenesis during which multiplication of spermatogonia occurs but the germ cells degenerate as soon as they develop beyond primary spermatocytes (Champy, 1913 ; Aron, 1926). The frog cycle is more closely related to the chelonian one, and spermatogenesis proper commences after a post-nuptial delay of some four to five months when the tubule lipids have largely cleared away (Lofts & Boswell, 1960).

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EXPLANATION OF THE PLATES

PLATE 1

Fig. 1—Testis of *Clemmys caspica* collected in January. Sertoli cells are elongating and filling the lumen of the seminiferous tubules. Spermatozoa have vacated the tubules and become stored in the epididymis. The only germ cells present are a peripheral ring of resting spermatogonia. (Bouin fixation ; iron haematoxylin and orange G ; sectioned at 6μ).

" 2—January specimen showing the dense lipid in the Sertoli cytoplasm. Interstitial Leydig cells also contain small lipid droplets. (Formal-calcium fixation ; Sudan IV and haemalum ; 8μ).

" 3—April. The densely lipoidal cytoplasm of the Sertoli cells now completely black the tubule lumen. Lipid droplets are still present in the interstitial Leydig cells. (Technique as in Fig. 2).

" 4—Testis in late April. Some spermatogonia are starting to divide. The Sertoli cells have continued to elongate and now completely black the tubule lumen. (Technique as in Fig. 1).

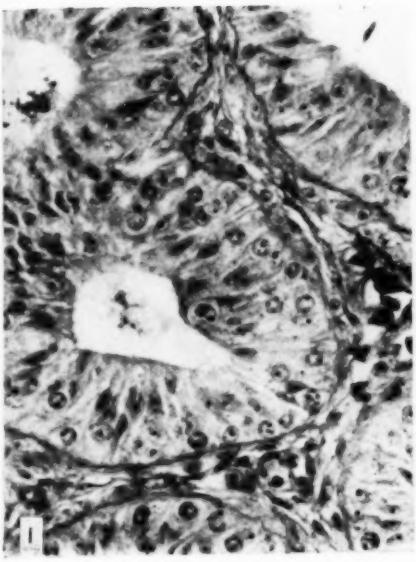
PLATE 2

Fig. 1—May. Spermatogenesis is now well underway. Most of the intra-tubular lipid has disappeared and only a few small droplets remain in the Sertoli cytoplasm. Interstitial cells are lipid free. (Formal-calcium fixation ; Sudan black and haemalum ; 8μ).

" 2—June. The seminiferous tubules are filled with actively dividing germ cells. Both tubules and interstitium are without lipid droplets. The latter contains relatively small juvenile Leydig cells. (Technique as in Fig. 1).

" 3—Epididymis of April specimen. There is a mass of spermatozoa in the canals. (Bouin fixation ; iron haematoxylin and orange G ; 6μ).

" 4—Epididymis of August turtle. Spermatozoa have been discharged and the canals have become reduced in size. As a result of the collapse, the canal wall has become thickened. (Technique as in Fig. 3).



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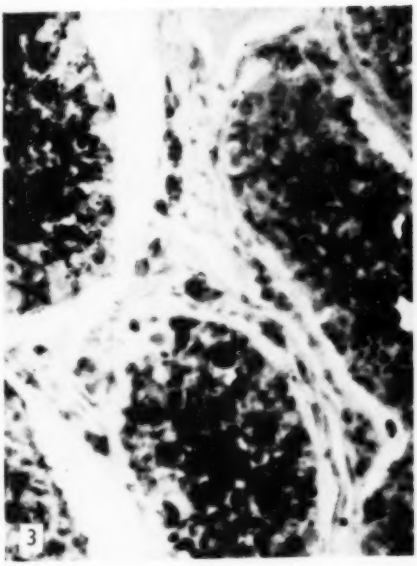
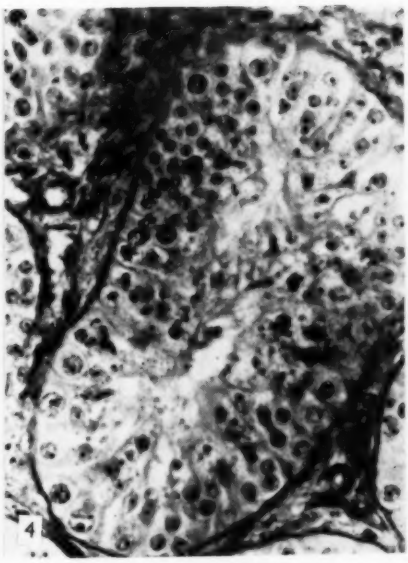
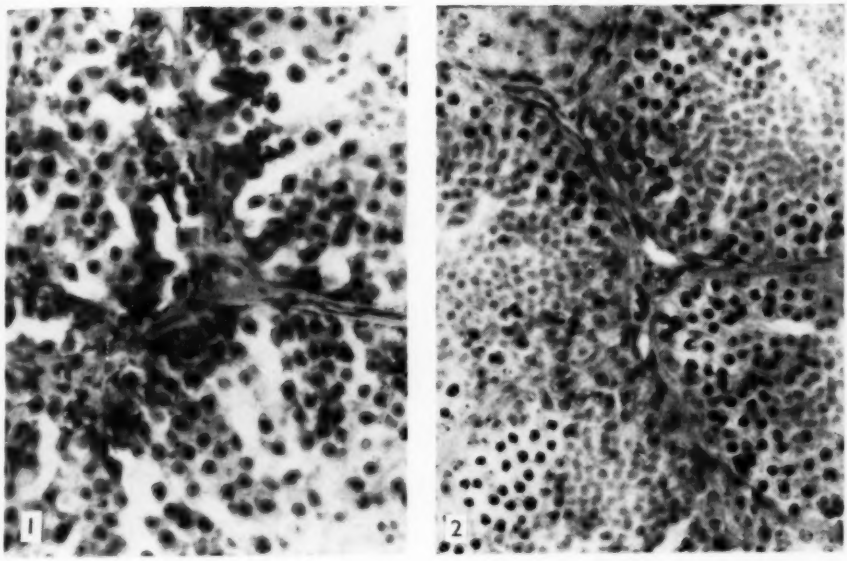
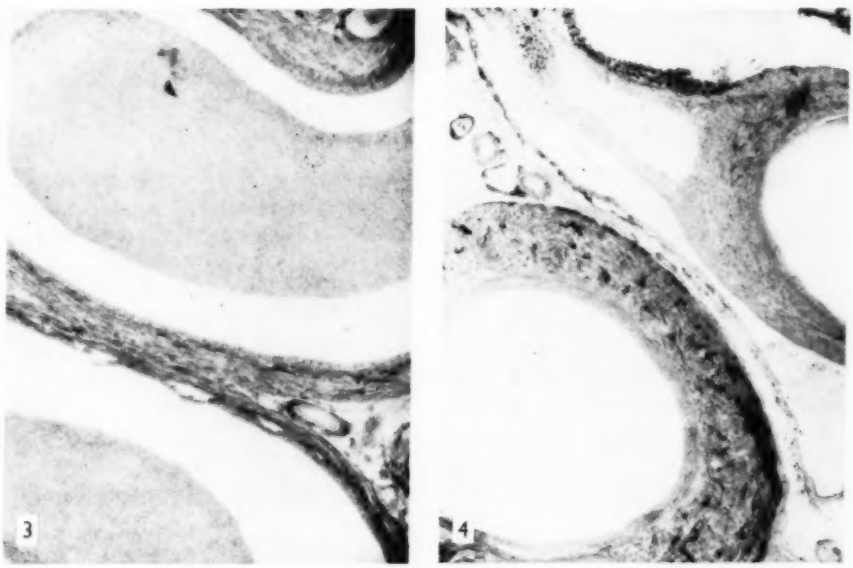




Seasonal changes in the distribution of the testis lipids of the Caspian terrapin.





Seasonal changes in the distribution of the testis lipids of the Caspian terrapin

ON A COLLECTION OF OESTRID LARVAE (DIPTERA) FROM EAST AFRICAN GAME ANIMALS

BY

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(With 6 figures in the text)

Eight species of oestrid larvae (subfamily Oestrinae), including an undescribed species of *Rhinoestrus* from the giraffe, from game animals in East Africa are described and figured. The tentative synonymy of the specific names given to these larvae and the adult stages is indicated. A key is provided to the genera of the third stage larvae of the subfamily Oestrinae from East Africa. Species of *Rhinoestrus* in Africa appear to be specific in their choice of mammalian host, but species of *Kirkioestrus*, *Gedoelstia* and *Oestrus* have been recovered from more than one genus of alcelaphine antelope. These antelopes are commonly parasitised by more than one species of oestrid. They do not, however, appear to be reservoirs of infection of *Oestrus ovis*, a common parasite of sheep and goats.

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INTRODUCTION

A collection of larvae of the subfamily Oestrinae (Zumpt, 1957) was made from game animals killed during 1946 and 1947, in the course of the Shinyanga Game Experiment around Old Shinyanga (3°33'S., 33°25'E.) and westwards to Izuka, in Tanganyika. Photographs of the district and a description of this environment are given in Buxton (1955). The oestrid larvae were collected from topi (*Damaliscus korrigum jimela* Matschie), wildebeeste (*Connochaetes taurinus hecki* Neumann) and giraffe (*Giraffa camelopardalis tippelskirchi* Matschie). This collection was presented to the Department of Entomology at the London School of Hygiene and Tropical Medicine by the East African Tsetse Research Organization and was added to other material, from alcelaphine antelopes, presented at various times to the Department by other collectors from Rhodesia, Tanganyika, Kenya and Uganda.

Recently Zumpt (1960) has studied the adult stages of oestrid flies from Africa and has reached certain conclusions about the synonymy. The present study of the collections of larvae from East Africa has also led, but by a different route, to a consideration of the problems of synonymy. One of the reasons for the complexity of synonyms in this family is that both adult and larval stages have

been given specific names. This is a temptation in a family where the parasitic larvae are found more readily than the very elusive adult flies. Another problem here is that the African antelopes of the subfamily Alcelaphinae usually carry mixed infections of oestrid larvae in the nasal and frontal cavities. Adult flies may be reared from some of these larvae and larvae belonging to another species may be retained as typical of the population bred out to the adult state. This has obviously happened in the past where the wrong larva has been ascribed to a reared adult fly.

Although one new undescribed species is obviously present in the collection of larvae described here, it seems as well not to give specific names to the early stages of these flies, with the possibility, if remote, that this might further confuse the already complicated synonymy within the family. For similar reasons, although the larvae are fairly easily distinguished from one another, specific names are given here only tentatively to those larvae that have been described before. Until the adult flies are associated with the complete puparia from which they have emerged, this synonymy must remain tentative. The collection does, however, show the presence in the host animals in East Africa of eight species of Oestrinae separable on larval characters, and belonging to four genera.

KEY TO GENERA OF LARVAE

Following Hennig (1952) and Zumpt (1957), the family, subfamily and genera can be separated on larval characters as follows :

Family **Oestridae**

Hind spiracles of larva with numerous pore-like openings (without slits or indications of slits).

Subfamily Oestrinae

Larval mouth hooks well developed (Fig. 1D) ; posterior spiracles deeply overhung dorsally by the rim of the last abdominal segment (Fig. 1B) and not visible from above ; larvae parasitic in the nose, frontal sinuses and pharynx of various Artiodactyla, and also in equids and the African elephant.

Key to the genera of the third stage larvae of the Oestrinae

1 (2). Hind spiracles distinctly emarginate to button along the inner edge, usually markedly so. (Fig. 1B)..... Genus *Rhinoestrus*.

2 (1). Hind spiracles more rounded and not obviously emarginate along the inner edge (Fig. 1E, 1F) 3

3 (4). Three groups of sensillae (" ocelli ") on each sensory lobe of the pseudocephalon ; hind spiracles often dissimilar in shape ..... Genus *Kirkioestrus*.

4 (3). Two groups of sensillae (" ocelli ") on each sensory lobe of the pseudocephalon (Fig. 1A) ; hind spiracles usually similar in shape 5

5 (6). Hind spiracles with dorso-ventral line from centre to lower margin, sometimes open and emarginate (Fig. 1E) ; no lobes lateral to posterior median group of spines ; small spines on segment I ascending laterally to the bases of the mouth hooks..... Genus *Gedoelstia*.

6 (5). Hind spiracles with horizontal line from centre to inner edge, usually not emarginate (Fig. 1F); or hind spiracles completely rounded with no trace of line; lateral lobes present on each side of the posterior median group of spines (Fig. 1B); no small spines ascending on segment I lateral to the bases of the mouth hooks (Fig. 4A, 5A, 6A)..... Genus *Oestrus*

In addition, two other genera of the Oestrinae are found in Africa: *Cephalopina* is found in the pharynx of camels and the third stage larvae may be recognised by the numerous pointed lobes ringing the body of the larva between bands of reduced spines (this genus is represented in the collections by larvae from the Sudan (D. J. Lewis) and Egypt (P. L. LeRoux)); *Pharyngobolus* is found in the pharynx of the African elephant and is also distinctive in the third larval stage with almost complete rings of spines, anteriorly and posteriorly, on most of the body segments (this genus is represented in the collections by larvae from Uganda (J. S. Perry)). (For illustrations of *Cephalopina* and *Pharyngobolus* see Rodhain & Bequaert, 1916 and 1919).

Genus *RHINOESTRUS* Brauer

Six species of *Rhinoestrus* have been described from Africa; three of these, *R. purpureus* Brauer, *R. steyni* Zumpt and *R. szlampi* Zumpt, parasitise equids (Zumpt, 1959); two species, *R. nivarleti* Rodhain & Bequaert and *R. phacochoeri* Rodh. & Bequ., are found in bush pig and wart hog respectively; and one species, *R. hippopotami* Grünberg, is recorded from the hippopotamus (Rodhain & Bequaert, 1916).

In the collection of larvae from Shinyanga there are many larvae of a *Rhinoestrus* from the giraffe, *Giraffa camelopardalis tippelskirchi* (Fig. 1A-D.) These larvae differ from other *Rhinoestrus* larvae described from Africa in the absence of rows of spines dorsally on the body segments posterior to segment I and in the presence of a well-marked ring of spines dorsally on segment I above the pseudocephalon (Fig. 1A). In some specimens small patches of spines are also present dorso-laterally on segments II and III but these are absent in other larvae. Only one *Rhinoestrus* larva known from Africa, *R. phacochoeri*, has the segments behind segment I devoid of spines dorsally but in this species segment I is also bare (Rodhain & Bequaert, 1916). *R. tshernyshevi* Grunin, which parasitises species of *Ovis* in Russia, also lacks spines dorsally except for some small spines above the pseudocephalon (Grunin, 1957), but the larvae from the giraffe differ in possessing more spines ventrally, from 50–60 spines in each of 4–6 rows on segments V-X (Fig. 1C), and by the presence of lateral groups of spines on these segments posterior to the ventral rows.

The species of *Rhinoestrus* are very specific in the hosts they parasitise and no other *Rhinoestrus* larva from any other host was present in the collection from Shinyanga except for one larva, resembling the giraffe *Rhinoestrus*, which was in a tube labelled " Roan, Left Hilltop, Captain Hilton, July 1946 ". This may have been an error during sorting the collection, either in Africa or in London.

No oestrid parasite has been recorded from the giraffe before, yet in the collection from Shinyanga there were 147 larvae from nine giraffes. Of these

forty-two larvae were labelled " from throat " and six were labelled " out of nose." Rodhain (1926) described two damaged oestrid larvae obtained from an okapi (*Okapia johnstoni* Sch.), the first kept in Europe, in the Zoological Gardens at Anvers. He ascribed these larvae, however, to the genus *Oestrus*, supposing them to be *O. ovis* L.

This larva from the giraffe represents an undescribed species of *Rhinoestrus* in Africa but until the adult fly is reared it is best left without a specific name.

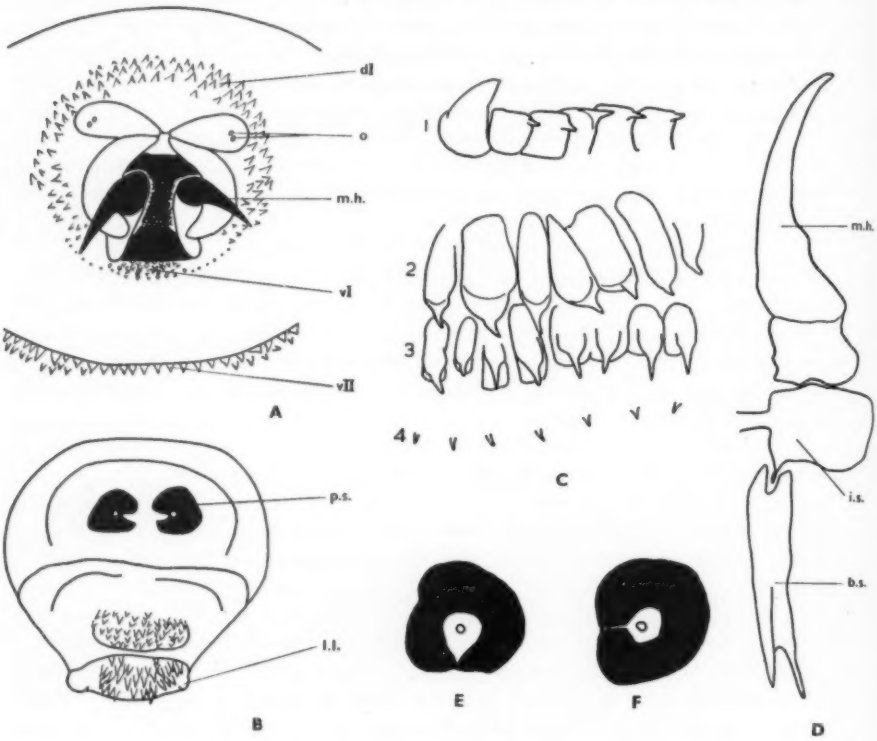

Fig. 1—A-D, Larva of *Rhinoestrus* from giraffe. A, Anterior view of larva ; B, Posterior view of larva ; C, Ventral spines on abdominal segment VI ; D, Head skeleton from above (right side only shown).

b.s., basal sclerite ; d.I., dorsal spines on segment I ; i.s., intermediate sclerite ; l.l., lateral lobe ; m.h., mouth hook ; o, " ocelli "; p.s., posterior spiracle ; v.I., ventral spines on segment I ; v.II., ventral spines on segment II ; 1, 2, 3, 4, rows of spines on segment VI ; E, Hind spiracle of *Gedoelstia* ; F, Hind spiracle of *Oestrus*.

Genus *KIRKIOESTRUS* Rodhain & Bequaert

No larvae of the genus *Kirkioestrus*, which are characterised by the presence of three " ocelli " on each lobe of the pseudocephalon, were present in the material from Shinyanga, but two species are represented in collections of larvae from Kenya and Uganda. Rodhain & Bequaert (1916) describe and

figure the larva of *K. surcoufi* Gedoelst, which has, in addition to the normal ventral rows of spines anteriorly on segments IV-X, lateral rows of large ventral spines posteriorly at the sides of these segments. A single larva, collected with larvae of *Gedoelstia* and *Oestrus* from the frontal sinuses of a hartebeeste, *Alcelaphus buselaphus* Pallas, in Uganda (J. S. Perry) agrees with this description (Fig. 2A).

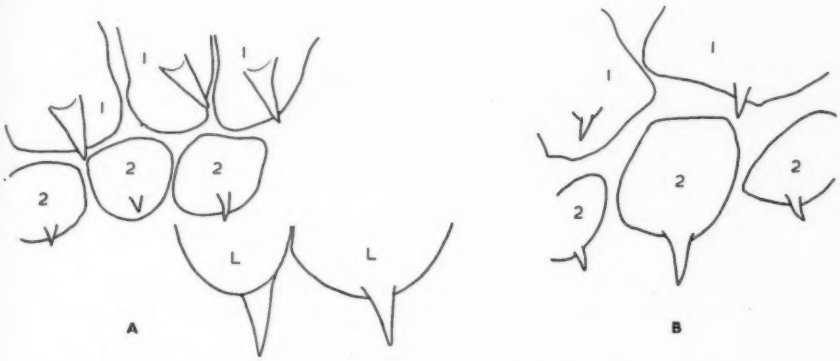

Fig. 2—Larvae of *Kirkioestrus*, ventral spines on segment VI. A, *K. surcoufi*? The posterolateral spines L are more posterior on the segment than shown here. B, *K. minutus*?

Other larvae with three " ocelli " were collected, together with larvae of *Gedoelstia* and *Oestrus*, from the sinuses at the bases of the horns of a hartebeeste, *A. buselaphus*, in Kenya (F. R. N. Pester) and these lack the posterolateral ventral spines on segments IV-X of *K. surcoufi* (Fig. 2B). The larvae are also smaller than the larva referred to *K. surcoufi*, although mature, and belong to a second species of *Kirkioestrus*, possibly to *K. minutus* Rodh. & Bequ. The larvae agree with the description of the larvae of *K. minutus* from *Alcelaphus lelwel jacksoni* Thom. and *Damaliscus korrigum jimela* Matsch. given by Rodhain & Bequaert (1916), although similar larvae in the British Museum (Natural History) Collection have been labelled by Gedoelst as *K. surcoufi*.

Genus *GEDOELSTIA* Rodhain & Bequaert.

Larvae of *Gedoelstia* proved to be the commonest oestrids found in alcelaphine antelopes from East Africa. Out of nineteen topi (*Damaliscus korrigum*) from Shinyanga, seventeen were infected by ninety-six larvae of *Gedoelstia*, compared with forty-two larvae of *Oestrus*. The larvae of this genus are characterised by the slit in the posterior spiracle being vertical, not horizontal as in the other genera (Fig. 1E) and the other characters given in the key help to separate this genus from *Oestrus* when the slit in the posterior spiracles is completely closed and not distinguishable. Two species of *Gedoelstia* can be recognised in the larval collections, one with two to three rows of spines ventrally on segments IV-X (Fig. 3A) and the other with three to five rows of spines ventrally on these segments (Fig. 3B).

The first species, which is similar to the description of the larva of *G. cristata* Rodh. & Beq. from *Alcelaphus lichtensteini* Pet. by Rodhain & Bequaert (1916), was found at Shinyanga only in *Connochaetes taurinus* (C. H. N. Jackson), but has also been found in *Alcelaphus buselaphus* in Uganda (J. S. Perry) and Kenya (F. R. N. Pester), and in *Alcelaphus lichtensteini* in Rhodesia (W. E. Ormerod).

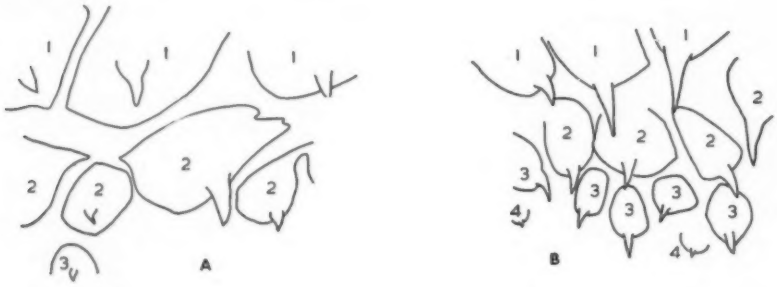

Fig. 3—Larvae of *Gedoelstia*, ventral spines on segment VI. A, *G. cristata* ? B, *G. hassleri* ?

The second species agrees with the description of the larva of *G. hassleri* Ged. given by Gedoelst (1916), and mentioned by van Emden (1945). This species has been found in *Damaliscus korrigum* from Shinyanga (C. H. N. Jackson) and in *Alcelaphus lichtensteini* from Rhodesia (W. E. Ormerod).

Genus *OESTRUS* Linnaeus

Three species of *Oestrus* from the nose and frontal sinuses of alcelaphine antelopes are represented in the collections. The three species are characterised by the arrangement of spines on segments I and II, and by the number of rows, and shape, of the spines ventrally on segments V-IX (Figs. 4–6).

One species is characterised by the presence of small spines or scales dorsally on segments I-III+(Fig. 6A) and four to five rows of spines ventrally on segments V-IX (Fig. 6B). This species agrees with the description of the larvae of *O. aureoargentatus* by Rodhain & Bequaert (1916) and with specimens labelled as this species by Gedoelst in the British Museum Collection. Larvae of this species have been found in *Damaliscus korrigum* in Tanganyika (C. H. N. Jackson), *Connochaetes* sp. in N.W. Tanganyika (collector not known) and *Alcelaphus lichtensteini* in Rhodesia (W.E. Ormerod). Rodhain & Bequaert (1916) also record this species from *Hippotragus equinus* Desm.

The larva of one other species of *Oestrus* from Africa also has rows of spines dorsally on segment I above the pseudocephalon but differs from the larva of *O. aureoargentatus* in that these spines are larger, not scale-like, and that the subsequent segments are bare dorsally (Fig. 5A). In addition the rows of ventral spines on segments V-IX are more numerous, five to seven rows on each segment, and these spines are more triangular and less abruptly pointed apically (Fig. 5B). This species is the same as specimens in the British Museum Collection labelled by Gedoelst as *O. macdonaldi* Ged. It is evident that *O. macdonaldi*

is not the same species as *O. aureoargentatus*, although this has been suggested by Rodhain & Bequaert (1916), and by van Emden (1945). Also in the British Museum Collection are two puparia attached to reared adult flies of

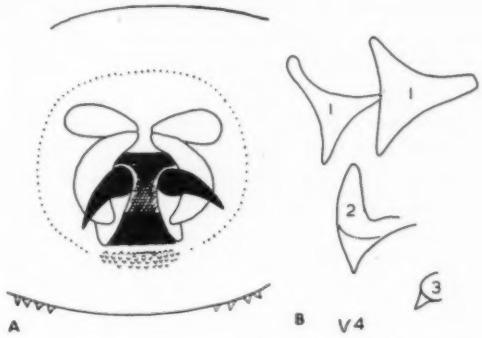

Fig. 4—Larva of *Oestrus variolosus* ? A, Anterior view of larva. B, Ventral spines on segment VI.

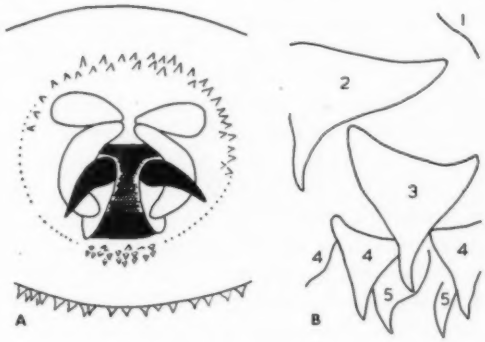

Fig. 5—Larva of *O. macdonaldi* ? A, Anterior view of larva. B, Ventral spines on segment VI.

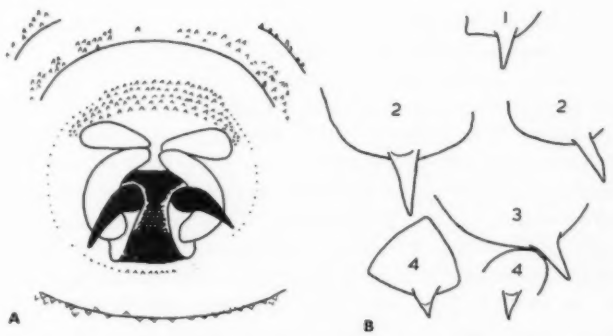

Fig. 6—Larva of *O. aureoargentatus* ? A, Anterior view of larva. B, Ventral spines on segment VI.

O. regalis Austen. These puparia have five to six rows of spines ventrally in segments V-IX, but the dorsal half of segment I in both puparia has unfortunately been lost after the emergence of the fly. It is possible that the larva with five to seven rows of spines ventrally on segments V-IX described by Gedoelst (1912) as *O. macdonaldi* is the early stage of *O. regalis* Austen (1934). The larva figured in Fig. 5A and B has been recorded from *Damaliscus korrigum* from Tanganyika (C. H. N. Jackson) and *Alcelaphus buselaphus* from Kenya (F.R.N. Pester). Gedoelst (1912) recorded *O. macdonaldi* from *A. lichtensteini*.

A third species of *Oestrus* from the Alcelaphinae is devoid of spines dorsally on segment I and on the segments posteriorly, and this species is also characterised by the row of spines ventrally on segment II being interrupted towards the mid-line (Fig. 4A). This larva also has three to five rows of spines ventrally on segments V-IX (Fig. 4B). The interrupted row of ventral spines on segment II distinguishes this species from the larva of *O. ovis*, from sheep and goats, where this row on segment II is complete.

These larvae agree with the description of the larvae of *O. interruptus* Gedoelst (1919), and also with specimens in the British Museum Collection labelled by Gedoelst as *O. bertrandi* Rod. & Beq. Also in the British Museum Collection are three puparia attached to reared adult flies of *O. variolosus* Lw. The dorsal half of segment I again is missing in these puparia but it is possible to make out on two of the puparia that the ventral row of spines on segment II is interrupted in the mid-line. There are also three to five rows of spines ventrally on each of the segments V-IX in all three puparia. Rodhain & Bequaert (1916) suspected that their *O. bertrandi* was really the larva of *O. variolosus*, which had been figured earlier by King (1911), and that the larva of *O. variolosus* described by Roubaud (1914) was really the larva of some other species. This larva described by Roubaud, with dorsal spines on segment I above the pseudocephalon, might belong to the species described by Gedoelst in the larval stage as *O. macdonaldi* (see above and Fig. 5A).

It thus seems probable that the larva with no spines dorsally on segment I and posteriorly, and with an interrupted row of spines ventrally on segment II, described as *O. bertrandi* and *O. interruptus*, is the larva of *O. variolosus*. The drawing by Terzi of the larva of *O. variolosus* in King (1911) agrees with this description. The larva with these characters is the commonest species of *Oestrus* in the larval collections and has been recorded from *Damaliscus korrigum* and *Connochaetes taurinus* from Tanganyika (C. H. N. Jackson) and *Alcelaphus buselaphus* from Uganda (J. S. Perry).

The three species of *Oestrus* described here are not specific parasites and have been recorded from three or more hosts amongst the alcelaphine and hippotragine antelopes. It is interesting to note that *O. ovis*, a common parasite of sheep and goats, has not been found in the collection from East African game animals and that these animals do not appear to act as reservoirs of infection for this species of *Oestrus*. Grunberg (1906) and Rodhain (1926) give some doubtful records of *O. ovis* from antelopes and okapi. It is not yet known if the larvae described here from antelopes are found in livestock in East Africa and this might well be investigated in sheep and cattle farming areas.

ACKNOWLEDGMENTS

It gives me great pleasure to acknowledge the help of Mr W. H. Potts, whose notes on the oestrid collection from Shinyanga made possible the description of the collection of oestrid larvae at the London School of Hygiene and Tropical Medicine.

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THE IMPACT OF PREDATION, ESPECIALLY BY THE TIGER-FISH (*HYDROCYON VITTATUS* CAST.) ON AFRICAN FRESHWATER FISHES

BY

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(With 1 figure in the text)

Study of *Hydrocyon vittatus* reveals that this fish, while a fierce and voracious predator, nearly always swallows the prey fish whole. Because of this the impact of predation is upon fish less than 40 per cent of the predator's length. The size structure of *Hydrocyon* populations is such that the main predation pressure is upon fishes of small size, the danger of predation becoming progressively less until a critical length, usually about 18–20 cm., is reached, above which a prey fish is reasonably safe from predation. The impact of predation is upon those fish which are mostly abundantly available to the predator, though these may not necessarily be the most abundant fish in the area. The use of cover, in the form of submerged vegetation or of very shallow areas of water, by fish which are small when adult or by the juveniles of larger species, is extensive. It is postulated that both the absolute number of fish and number of fish species which are small when adult, in an area inhabited by *Hydrocyon vittatus*, and possibly also *Lates niloticus* subspp., is governed by the amount of vegetal cover available throughout the year and that the spawning migrations of fishes, being found only among those species or very closely related species, which are or have once been in contact with these voracious predators, is primarily undertaken in order to place the young in an environment where refuge from these predators is available. The view that the presence of these predators has the effect of retarding speciation is supported.

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INTRODUCTION

The tiger-fish, *Hydrocyon vittatus* Castelnau, has attracted attention for many years both because it is always a striking member of any fish fauna which includes it, and because of the effect that its ferocity as a predator may have had upon the evolution of African fishes. With regard to the latter, its name (and those of other members of the genus) is usually linked with those of the genus *Lates* Cuvier, the Nile perches of North and Central Africa. The ecology of neither of these genera has been very extensively studied ; indeed Greenwood (1957) says of *Lates niloticus albertianus* Worth. that Worthington's (1929)

study remains the most comprehensive account, despite the great importance of this fish. Discussions particularly of the effect that these genera have had on the ecology and evolution of other fish have therefore remained largely speculative, and indeed to obtain any evidence of the impact that they have had on other fishes has seemed at times to be difficult.

Following studies of *Hydrocyon vittatus* in the Middle Zambezi river (Jackson 1961a), it seemed that some progress in this direction could be made because of the simple fact that *H. vittatus* swallows its food whole. Its teeth are used for biting and holding, not cutting, so that in nearly all cases the tiger-fish bites and turns its prey, prior to swallowing it, head first, whole. Swallowing the prey whole seems, so far as is known, a feature of all African freshwater predatory fishes, although of course it is by no means so in all fishes. In the case of the tiger-fish, this fact means that the prey in the stomach contents can not only often be identified even to species, but also that its length can in many cases be measured. This was then a way whereby some data could be obtained on the impact of its predation on other fish, as there are very few recorded cases of *H. vittatus* biting chunks out of anything.

The phenomenon of swallowing the prey whole means that *H. vittatus* must prey on fish much smaller than itself ; the extreme upper limit is less than 50 per cent of its own length, but this does not mean that the reputed ferocity of the fish has been at all exaggerated. This ferocity has had much tribute paid to it. Quoting from McCormick (1949) is not to be resisted : " I have stated heretofore in print, and am still ready to maintain my pronouncement, that the tiger-fish of Africa is the fiercest fish that swims. Let others hold forth as advocates for the mako shark, the barracuda, the piranha of the Amazon, or the bluefish of the Atlantic. To them I say, ' Pish and tush ' " (p. 349). Greenwood (1956) states " there are few accounts of African sporting fishes which have not their purplest patches almost breathlessly eulogising the tiger-fish " (p. 37). Indeed the ferocity of these fishes must be seen to be believed. Species of *Lates* in Lake Tanganyika seem also to cause great alarm to smaller fishes. Offshore, here, a mass of small fish breaking water in a flurry of foam is a frequent sight. It is reminiscent of the sights seen by a marine biologist, but the sister lake, Nyasa, presents no such spectacle.

Despite the known ferocity of *Hydrocyon*, there is some tendency to pay lip service to it and go on to discuss predation in African fresh waters as though all predators were equal in their impact. In fact the variation in degree of predation, perhaps especially the degree in which the life of the surviving prey is disturbed, is as great in African freshwater predators of several genera as it is in many other animals. Though some shrikes are known to include other birds in their diet, no one would say that the impact of predation of the Laniidae and Falconidae upon other birds are equal.

Evidence will be assembled in this paper towards the view that while *Hydrocyon vittatus* affects other fish by direct predation on them, it also greatly influences their life history as a result of this predation. It seems probable that many of the spawning migrations which are so marked a feature of the life-histories of many African freshwater fishes are directly influenced by the

impact of predation by this fish. Indeed I go further and postulate that some of the anadromous migrations into rivers from lakes which do not now, or perhaps never did, hold stocks of *Lates* and *Hydrocyon* is because of the effects of predation on bygone generations which did feel the impact of these fishes, far-fetched as this concept seems at first sight to be.

TAXONOMY AND DISTRIBUTION OF *HYDROCYON VITTATUS*

I here follow Barnard (1948) in using Castelnau's specific name of *vittatus* (1861), rather than the name *lineatus* of Bleeker (1862).

The species is one of the larger rivers and lakes ; it is not found in small streams, except in so far as it seasonally penetrates them for spawning, nor in swampy marshes except where there is a flow of well-aerated water through them, such as a large water-channel through a swamp. It has a wide distribution in tropical Africa, with some remarkable discontinuities. It is found in most of the larger river systems, such as the Nile, Niger, Volta, Congo, Zambezi and Limpopo. Its furthest southerly limit is the Mkuzi river which flows into Lake St. Lucia, Natal (Jubb 1952). It occurs in Lakes Albert, Rudolf, Tanganyika, Mweru and Bangweulu. Among its more notable absences are from Lakes Nyasa, Rukwa, Edward, George and Victoria, and their watersheds, and also from the large Kafue river which flows into the Middle Zambezi system.

OBSERVATIONS ON THE FEEDING HABITS OF *HYDROCYON VITTATUS*

There are very few cases known to me of *Hydrocyon vittatus* attacking any animal larger than half its own length. Many anglers in tropical African waters have tales of fish being mutilated or bitten in half while on the hook, these depredations often being attributed to very large tiger-fish. Perhaps, however, otters or crocodiles might sometimes be the culprits. In my own experience, I have once removed a *Labeo altivelis* Peters of 21 cm. from a 45·5 cm. *Hydrocyon vittatus*, which was severed in two, the halves lying side by side in the stomach. The line of severance was a neat cut at right angles to the body, and it was not possible to tell whether it had been done by the *Hydrocyon* which swallowed the fish or not. In October, 1956, at the height of the dry season, a young crocodile about six or seven feet long was shot in the head by an Express rifle in a pool in the Sanyati river, Middle Zambezi system. While instantly killed, it floated for a minute or two, emitting large quantities of blood from the wound which stained the water all around. A number of large *Hydrocyon* were instantly on the spot, questing savagely through the blood and biting at the wound. The crocodile sank and the scene was over as suddenly as it had begun. On a third occasion, during the stocking of the new lake Kariba with *Tilapia macrochir* Blgr., I watched for some hours an unfortunate shoal of these fish, from 10 to 15 cm. in length, which had in error been released on an open beach and not among submerged vegetation. The fish, which had been bred in ponds from stock originally from the Kafue river (where there are no *Hydrocyon*), were completely helpless on first release. They huddled together in the shallowest water at the edge, while from time to time young tiger-fish of about 25 cm. would pass rapidly

through, biting one here and there in passing ; they were too large to be seized and swallowed. Periodically one would die, and I retrieved several of these. Most had tooth wounds in the body but had no sign of pieces bitten out, but one had the tail and part of the caudal peduncle missing. Endemic *Haplochromis darlingi* Blgr. were in the same locality but quite at home there, dodging under rocks when necessary. After several hours the *Tilapia macrochir* began to find their way to suitable refuges and by evening no further mortality was observed.

It seems in general that the habit of savaging large animals, biting things in half, etc., if it occurs at all, is done by exceptionally large specimens. I have heard of large specimens from anglers, and the Northern Rhodesia Fish Records Association lists the present rod and line record for *H. vittatus* as 22 lb., caught in the Middle Zambezi on 30th October, 1959. It is my misfortune, however, never to have come across any of the very large fish spoken of by anglers. Of several thousand specimens seen in the field, the largest in my personal experience was just over 11 lb., from Lake Tanganyika. From the Bangweulu area the largest that I have seen was 10 lb., and from the Zambezi 8 lb. 9 oz. All these had orthodox stomach contents. I conclude that the bulk of any *Hydrocyon vittatus* population is 55 cm. in length or 3 kg. (6½ lb.) in weight or less, so that the greatest amount of predation pressure is caused by fishes up to this size. Fishes larger than this are so comparatively few as not to have any significant impact of predation, especially on the immature stages of prey. I make the assumption also that the situation is broadly similar with regard to this species where it occurs in those areas where I have not worked, that is, south of the Zambezi and north of Lake Tanganyika.

All evidence so far shows that the preferred food, from a length of about 5 cm., is fish. Studies in the Middle Zambezi showed (Jackson 1961a) that in the hot dry months of the year, when the volume of flowing water was enormously reduced in comparison with the rainy season flow, food taken by *Hydrocyon* even of 30 cm. or more in total length changed to include a very large insect component. This was due to the river, when sunk to this low level, being ecologically unfavourable to small fishes in that cover from predators was absent and food reduced in quantity, so that the total number of fishes small enough to be swallowed whole by tiger-fish of these lengths was reduced below the level sufficient to supply the needs of the predator population. As it is not the normal habit of *Hydrocyon* to prey on larger fish by biting pieces out of them, the smaller predators had perforce to change largely to an insect diet.

Records from Lake Bangweulu and its adjacent swamps show no such large seasonal change in diet. Table 1 gives records since 1951, which shows that out of a total of 1023 stomachs which had food of some sort (most, especially gill-netted fish, are empty) only fifty-one were of components other than fish. Of these records forty are of the freshwater prawn (*Caridina nilotica*), seven are of vegetation (grass is specified in two instances), while five are of " insects " not further specified. It can be seen that for the six months covering the rainy season, that is from November to April inclusive, twenty non-fish stomach components were recorded, as against thirty-one for

Table 1—Numbers of *H. vittatus* containing fish (left-hand figure) and food other than fish (right-hand figure), by monthly totals of specimens examined in the years 1951–1959, Bangweulu area.

Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	
									26/1	10/1	12/0	1951
					1/0	8/0	9/2	19/3	18/2	7/1	24/0	1953
25/1	2/0	8/1	3/0									1954
13/0	40/2	21/1	18/1	30/2	27/4	21/3	22/0	27/1	13/2	16/0	35/1	1955
22/0	25/1	6/0	21/0	4/0	0/0	3/0	3/1	18/3	0/0	6/0	11/2	1956
6/5			10/0	2/1	12/0	20/0	13/0	31/0	38/0	3/0	1/0	1957
7/1	0/0	3/0	18/1	31/0	14/0	19/1	10/1	37/0	28/0	8/0	13/0	1958
1/0	22/0	2/0	6/1	13/0	10/1	24/1	15/1	7/0	11/1	10/0	4/0	1959
74/7	89/3	40/2	76/3	80/3	64/5	95/5	72/5	139/7	134/6	60/2	100/3	

the six dry months of the year. This slight seasonal increase in the non-fish diet may be contrasted with the very large seasonal increase in the Middle Zambezi mentioned above. This contrast can be attributed to the fact that in the large permanent Bangweulu lake and swamps, with a small annual rise and fall (about five feet as opposed to thirty and more in the Middle Zambezi before inundation by Kariba), adequate cover and food exists all the year round for small fish. Far more small fish exist, both juveniles and especially those which are small when adult, at all periods of the year than was the case in the Middle Zambezi. For this reason there is a better continuous balance between predator and prey, predator numbers being smaller in relation to the total amount of prey than was the case in the adverse period in the Middle Zambezi.

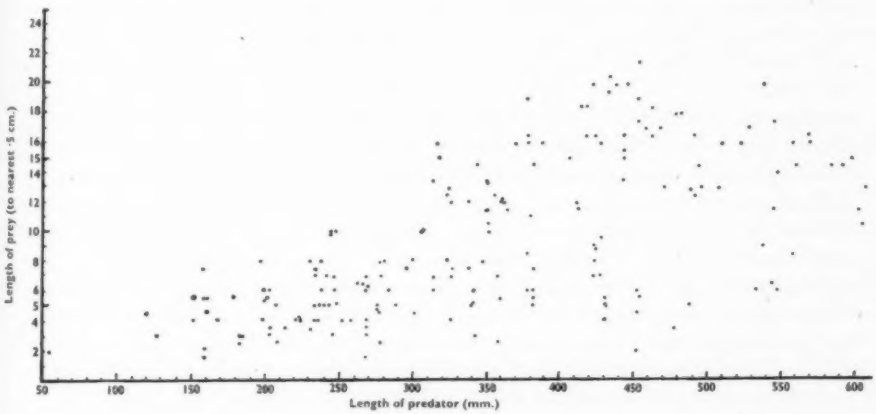

Fig. 1—Scatter graph showing the length of the prey fish (for all prey species found) in relation to the length of the *Hydrocyon vittatus* in whose stomach the prey was found. Data from Bangweulu, Mweru and Middle Zambezi areas.

The size of prey in relation to the size of predator is given in Fig. 1 for 188 *Hydrocyon vittatus* with measurable prey in the stomach. It can be seen that in no case is the prey greater than 50 per cent of the size of the predator,

and only exceptionally is it greater than 40 per cent of the predator's size. Secondly it can be seen that while it follows from this that small *Hydrocyon* eat fish of small size, such smaller fish are often taken by much larger tiger-fish, the range of prey size in the larger predators being wide. Thirdly the graph shows that fish over 18·5 cm. in length figure rarely in the diet of *Hydrocyon vittatus*. The reason for this is that the bulk of any given population of this species is of a size where larger fish cannot be swallowed whole, as is the almost universal habit. Theoretically, given a predator length of 55 cm. as a significant maximum and a prey length significance of 40 per cent, the prey maximum would be 22 cm. In practice in Central Africa it seems rather less than this, as the graph shows. But a length of what may be broadly reckoned as between 14–20 cm., considering all species of fish together, seems to be critical in the life-history of many African freshwater species not endemic to the Great Lakes, and it crops up often in such ecological studies as have yet been done. Fish often change their habitat at this stage ; see, for example, Jackson (1961a) for the Middle Zambezi fishes, and the case of *Tilapia macrochir* in Lake Mweru cited below. Again, Lowe (1959) states that " in Lake Albert (and possibly also in Lake Rudolf and Lake Tanganyika) 12–18 cm. *Tilapia* are found inshore and some *Tilapia* remain inshore and in lagoons round the lake for all or most of their lives " (p. 9), and rightly assumes that this appears to be associated with the presence of the predators *Lates* and *Hydrocyon* in these lakes.

Prey species in the Bangweulu area are shown in Table 2. Here, as in Table 1, records from Samfya on the western shore of Lake Bangweulu and from various points in the Bangweulu swamps are combined. This gives a general picture and is so far just in that these areas are not geographically separate and that there are very few fish species which have not been recorded both from the lake and the swamps, but care must be taken not to fall into that old pitfall of workers on African lakes, the failure to recognize preferences among fish for distinct ecological zones. Thus *Serranochromis angusticeps* (Blgr.) is a fish which prefers deepish water heavily overgrown with water lilies and other vegetation, and is thus much more abundant in the swamp channels and lagoons than it is in the lake itself, and the three identifications of this fish as a prey are all from swamp stations. Again *Tylochromis bangwelensis* Regan is physiologically tied to well-aerated water, being extremely sensitive to oxygen lack, and is thus more common in the lake than the swamps. With these reservations in mind it can be seen that records from the area in general show a fairly wide range of prey species but that over 40 per cent of the total is of fishes of the family Cichlidae. The impact of predation is next greatest on the family Characidae, with the single species *Alestes macrophthalmus* Gunther comprising over a fifth of the total.

There are as yet no figures of the relative abundance of species in the Bangweulu area, but it is probable that the first two species in the list, *Alestes macrophthalmus* and *Tylochromis bangwelensis*, are among the most generally abundant in the area, being very closely rivalled however by the cyprinodont *Aplocheilichthys moeruensis* Blgr., the cichlid *Tilapia sparrmani* Smith and the cyprinid *Barbus banguelensis* Blgr. It is significent that no cyprinodonts

Table 2—Species and percentages of 184 fish taken from the stomachs of *Hydrocyon vittatus* in Lake Bangweulu and the Bangweulu swamps.

Prey species	Number	Percentage
Alestes macrophthalmus	38	20·7
Tylochromis bangwelensis	25	13·6
Cichlid species	21	11·4
Barbus species	13	7·1
Alestes species	10	5·4
Barbus banguelensis	10	5·4
Tilapia species	8	4·3
Synodontis nigromaculatus	7	3·7
Sargochromis mellandi	7	3·7
Alestes grandisquamis	6	3·3
Cyprinid species	5	2·7
Barbus paludinosus	5	2·7
Tilapia macrochir	4	2·2
Serranochromis angusticeps	3	1·6
Haplochromis moffatii	3	1·6
Gnathonemus species	3	1·6
Engraulicypris moeruensis	2	1·1
Tilapia melanopleura	3	1·6
Hydrocyon vittatus	2	1·1
Tilapia sparrmani	2	1·1
Mormyrid species	2	1·1
Clarias species	1	0·6
Characid species	1	0·6
Serranochromis species	1	0·6
Distichodus maculatus	1	0·6
Alestes imberi	1	0·6
Total	184	100·0

were recognized during examination of *Hydrocyon* stomachs ; the reason probably is that they live in surface waters among dense grass and other vegetation. On the other hand both *Tylochromis bangwelensis* and *Alestes macrophthalmus* are among the most open-water living species known in the Bangweulu region. *A. macrophthalmus* is widespread in shoals in rivers, lagoons and the open lake shore, the juveniles in the more inshore, shallow localities with the adults further out. I am informed by my colleague Mr D. Harding, who is making a study of *Tylochromis bangwelensis*, that, apart from its striking preference for well-aerated waters, it is a fish of open sandy beaches, the juveniles keeping inshore among vegetation, with adults further out if there is a sandy substrate, the fish in general according to his observations occupying the same sort of niche in Lake Bangweulu as species of the genus *Lethrinops* Regan do in Lake Nyasa. *Lethrinops* of course form a species-flock with twenty-four species at present described, but only one species of *Tylochromis* is known each from Lakes Bangweulu, Mweru and Tanganyika.

Barbus species, in spite of their being very abundant both along the lake shore and in swamp and river channels, at least seventeen species having been recorded, figure less largely than might be expected, with only two species

identified in the prey, so that even such abundant and well-marked species as *B. trimaculatus* Ptrs. and *B. multilineatus* Worth. have not been identified as prey. Finally *Clarias mossambicus* Ptrs. is an abundant fish in the area but only one clariid specimen is recorded. Adult *C. mossambicus* are of course far too large to fear the tiger-fish and there is evidence that juveniles are spawned in streams away from the lake (see Greenwood 1955 and below).

More data of this kind are required, and more in general needs to be learned of the ecology and relationships of African fresh-water fishes, but without going into further detail it can be concluded that *Hydrocyon vittatus* will prey on those species which it encounters most frequently, subject to their availability. In some cases these may be the most abundant fishes present, but almost equally abundant species may escape predation by adopting a habit of sheltering among thick vegetation or other cover either all their lives or in the juvenile stages, others may, as a result of migration by the parents, pass the vulnerable stages or in a refuge or habitat that the predator cannot reach.

FISH MIGRATIONS AND THE NECESSITY FOR COVER

Even with our present limited knowledge of the ecology of African fishes it is apparent that many species undergo spawning migrations, with the result that eggs are hatched in a place other than that normally occupied by the adults. The view is here put forward that this is in order to enable the young to exist where conditions of cover and food are favourable, and is largely made necessary for the avoidance of predation, especially by *Hydrocyon vittatus*.

There are so many examples known of the end stage of an African fresh-water fish migration being in an environment suitable as a refuge that it seems extremely probable that one of the specific purposes of the spawning migration is to provide a refuge for the young fish. A most interesting example is that of the cichlid *Tilapia macrochir* in Lake Mweru. Here it is an extremely valuable commercial fish, known to the native fishermen as " Mpale ". The adult " Mpale " are shoaling and live in open waters of the lake, where they are caught in large numbers. It is well known to the local Africans, however, that the juveniles live in another place, along the swampy southern edge of the lake. These juveniles are called another name, " Kakenje ", although it is recognized that the two are of the same species, so the Africans are aware that a " Kakenje " is a young " Mpale ". In 1958 the breeding grounds were investigated, and found to be behind and among the large thick banks of " hippo grass " (*Vossia cuspidata*) which are in profusion along the southern shore. In several places, such as along the eastern shore of Isokwe Island, Lake Mweru, the *Vossia* grows in a wide belt, between which and the shore, when the lake level is high, is a narrow strip of water, sometimes artificially enlarged by the inhabitants of native fishing camps and villages to provide a harbour for canoes. One such place was seined with a small ($\frac{1}{2}$-inch $\times$ 30 yards) net on the 31st March, 1958, when a single haul yielded 144 young *Tilapia macrochir* of lengths between 3·5 and 16·0 cm., with modes at 9 and 14 cm. No larger fish were taken. Another haul in the same place on 13th June, 1958, gave 231 juveniles with a large mode at 4·5 cm., another at 14·5 cm. and a third at 19·5 cm. There were two fish of 23 cm. and one of 24·5 cm., but no large adults at all.

On both occasions seine hauls on open lake beach within a mile of the area yielded some large but no juvenile *T. macrochir*, while gill nets set in open water caught adults up to 40 cm. in length.

It seems from this preliminary work (which it is hoped shortly to continue) and from the opinions of African fishermen that there is a spawning migration of *Tilapia macrochir* from the open waters of the lake, one of the end results of which is to place the young fish in the cover of *Vossia cuspidata* and other swamp vegetation. At a length of about 18–20 cm. the young fish enter the open water, when they are no longer called " Kakenje " by the fishermen.

Vossia is also a habitat for many other fishes in this area, as pointed out by Jackson (1959). Table 3 gives a list of fishes which have so far been discovered in Lake Mweru in among the dense mats of this grass. Fish in the first column are found there when juveniles and none, apart from the few *T. macrochir* mentioned above, have yet been found of a length greater than 18·5 cm. The second column is of fish which are found among the grass in the adult stage. There is little doubt that the advantage of living among *Vossia* is two-fold ; there is an abundance of insect, crustacean and other food, and there is complete protection from large predators, especially *Hydrocyon vittatus*. It is significant, with regard to the latter, that the fish in the second column, which spend all their lives either in or so near this vegetal cover that it can be used as a refuge at will are all small (never more than 20 cm. and usually less) when adult.

Table 3—Fish species thus far discovered in belts of the grass *Vossia cuspidata* fringing the southern open shores of lake Mweru.

A. Species found in *Vossia* when juvenile.	B. Species found in *Vossia* when adult.
Tilapia macrochir Blgr.	*Aplocheilichthys moeruensis* Blgr.
Chrysichthys mabusi Blgr.	*Mastacembalus moeruensis* Blgr.
Synodontis unicolor Blgr.	*Barbus brevidorsalis* Blgr.
Serranochromis robustus (Gthr)	*Clarias theodorae* Weber.
Serranochromis angusticeps Blgr.	*Haplochromis moffatii* (Cast.)
Mormyrops delicosus (Leach)	
Mormyrus longirostris Pters.	

There are other known examples of spawning migrations in African waters other than the Great Lakes. These are of varying length and duration, and vary in other details from place to place, but the end point invariably is that the young fish are to be found in shallow and sheltered water, with an abundance of vegetation. Matagne (1950) has described the spawning migration of *Labeo altivelis* in the Luapula River. Before the fish were decimated by overfishing this migration was a well-known phenomenon on the river, known as the " Kapata " when solid masses of ripe fish used to move along the river, and the same pattern is still followed, though not in the same numbers as before. The spawning occurs in the first months of the year, when the river comes down in spate after the rains are established and floods over its banks into the adjacent low-lying flood plains which are covered with long grass and other vegetation. *Labeo altivelis* then leaves the river and the eggs are laid among grass in the flood plains and in sheltered tributary streams. Here the

young probably live until the lowering in level of the river as the dry season progresses forces them back into the main stream. By then, however, the juveniles are well grown and by the end of the first year of life they have probably reached a size of 16–18 cm., when there is little danger of predation from all but the largest *Hydrocyon*.

Greenwood (1955, 1957) shows that *Clarias mossambicus* migrates out of the main waters of Lake Victoria in order to spawn in small temporary streams during the rains. The same behaviour has been noticed in Lake Bangweulu where very large catfish of this species are speared by fishermen in relatively tiny streams on one or two days only, during the rains. Jackson (1961a) has described how, in the Middle Zambezi during the rains, almost all species move out of the main river and spawn in sheltered flooded creeks, plains and oxbows away from the main river. These places invariably have much submerged vegetation. Whitehead (1959) has shown that in rivers affluent to Lake Victoria a number of lake fishes regularly ascend flooding rivers in order to breed. Bell-Cross (1960) has shown that twenty-four out of thirty-one species known to inhabit a Northern Rhodesian river migrated upstream during the rains. Soulsby (1960) states that *Hydrocyon vittatus* migrates up the Luapula river out of Lake Mweru in January each year, at the height of the rainy season.

While a very great deal remains to be learned, the evidence all shows that, apart from the endemic and more lately evolved Great Lake species, eggs are laid in almost every case in an environment where the risk of predation by the adult *Hydrocyon vittatus* is at a minimum. The same does not necessarily follow in the case of other and milder fish predators. *Serranochromis angusticeps*, for example, is, as already said, a fish of stagnant weedy waters ; in the clear channels of the Bangweulu swamps it can be seen diving in and out of a heavy growth of water weeds, a habitat in which the open-water *Hydrocyon vittatus* is never found, as it always remains outside of such weed-banks in the swamp channels. *H. vittatus* is, moreover, never to be found among the banks of *Vossia* grass, even when juvenile, unlike the young of three minor predators which are listed in Table 3, namely *Serranochromis robustus*, *S. angusticeps* and *Mormyrops deliciosus*.

The reason why *Hydrocyon vittatus* is not to be found in such thick and dense vegetation is probably to do with its fierce and dashing habit of life, in contrast with what Lowe (1959) has aptly described as " lurking " (rather than " swift ") predators. The young of the tiger-fish have naturally however the same need of protection from predation as those of other species, and a spawning migration up rivers out of lakes, and into tributary streams, is followed by this species also. Apart from the evidence given in Jackson (1961a), very young juveniles of 1·3 cm. have been found in shoals in the Mulobezi river (tributary of the Middle Zambezi in the area now being flooded by the Kariba dam). These were in tight shoals where the river was three to six feet wide and six inches to two feet deep, quite stagnant due to the height of the water into which the tributary led, and well but not thickly overgrown with reeds and other vegetation. These little fish followed a usual evasion pattern by scattering in all directions when attacked with a hand net.

Table 4—Summary of habits and spawning activity of typical Central African fish, other than endemic Great Lakes species.

BROAD HABITAT	TYPICAL SPECIES	TYPICAL SPAWNING BEHAVIOUR
	Never exposed to *Hydrocyon vittatus*	
Small streams	*Amphilius platychir* (Gthr.)	Under stones in currents ; no migrations known.
	Barbus lineomaculatus Blgr.	?. Upstream migrations occur, perhaps for distribution, not spawning.
	Kneria auriculata (Pell.)	?. Ditto.
	Barilius neavii Blgr.	?. Ditto.
	Clarias submarginatus Ptrs.	?. Ditto.
Shallow marshes	*Barbus paludinosus* Ptrs.	?. May be upstream movements after rain.
	Barbus multilineatus Worth.	?. No movements known.
	Barbus haasianus David	?. Ditto.
	Aplocheilichthys spp.	?. Probably no movements unless water dries up.
	Adults exposed to *Hydrocyon vittatus* at times (e.g. flood)	
Large swampy marshes, often connected to large rivers or lakes	*Clarias mossambicus* Ptrs.	Spawns in shallow streams and inlets.
	Tilapia melanopleura Dum.	Spawns in shallow weedy water ; no migrations known.
	Gnathonemus macrolepidotus Ptrs.	?. Migrations known in Bangweulu.
	Haplochromis moffatii (Cast.)	Spawns in shallows ; no migrations known.
	Petrocephalus simus Sauv.	?. Lives in weedy water.
	Aplocheilichthys spp.	?. Upper layers of weedy water.
	Barbus afrovernayi N. & B.	?. Lives in weedy water.
Waterfalls and rapids, stony substrates	*Euchilichthys* spp.	?. Highly specialized to waterfalls, some movement known.
	Chiloglanis neumanni Blgr.	?. Specialized to rapids ; migrations not known.
	Labeo annectens Blgr.	Spawns where cover provided by rocks.
	Adults permanently exposed to *H. vittatus*	
Rivers, lagoons, lakes, channels in large swamps	Populations 20–100 species with three spawning habits :	
	(i) *Labeo altivelis*, large *Barbus* spp., *Hydrocyon vittatus, Distichodus mossambicus* Ptrs., *Clarias mossambicus, Tilapia mossambica*	Migrations to flood-plains of rivers and flooded streams during rains.
	(ii) *Tilapia macrochir, Mormyrops deliciosus, Chrisichthys mabusi, Serranochromis* spp., *Clarias theodorae, Synodontis* spp.	If not a permanent inhabitant, moves to shallow banks and water edges, near vegetation.
	(iii) *Pellonula acutirostris* Blgr., *Engraulicypris moeruensis* Blgr., *Barbus banguelensis, Alestes macrophthalmus.*	Adults live in offshore or pelagic shoals. *Pellonula* and *Engraulicypris* probably have pelagic eggs and larvae, others move inshore or up rivers to spawn.

The spawning behaviour of Central African fishes other than Great Lake species, so far as is known, is summarized in Table 4. The number of queries in the table is an indication of our present limitations of knowledge, but there is no evidence of any fish spawning where cover and refuge from *Hydrocyon vittatus* does not exist.

The necessity of cover in general for Central African fishes is shown in Table 5. It can be seen that in three neighbouring but ecologically distinct areas, the Upper and Middle Zambezi and the Kafue, the first and last, which both have large reservoirs of water in the form of swamp and flood-plain which release the annual rainy-season's water gradually, thus providing considerable vegetation throughout the year, have both the total number of fish species and the number of those which are small (less than about 18–20 cm.) when adult more numerous than is the case in the Middle Zambezi. This river, though the Upper Zambezi flows into it, has because of the great length of the Zambezi as a whole and because the Middle Zambezi flows through a low-rainfall area, no such reservoir in the dry season, and as a result sandbanks bare of vegetation predominate at this time, while the flood is violent and of comparatively short duration. The paucity of species reflects these seasonal adverse conditions. The very low percentage of species which are small when adult is probably a measure of the impact of predation by the tiger-fish, and it is perhaps significant also that the Kafue, which alone of the three has no *Hydrocyon* population, has the largest percentage of species which are small when adult.

Table 5—Summary of ecological conditions, number of species and percentage of those small when adult in the Middle Zambezi, Upper Zambezi and Kafue rivers (data from Jackson (1961a) and a check-list of fishes of Northern Rhodesia, in preparation).

UPPER ZAMBEZI (Above Victoria Falls)		MIDDLE ZAMBEZI (Between Victoria Falls and Kebrabassa Rapids)		KAFUE	
Extensive swamps and flood-plains; vegetal cover throughout year		No swamps, small flood-plains; vegetal cover absent for part of year		Extensive swamps and flood-plains; vegetal cover throughout year	
Total fish species	72	Total fish species	28	Total fish species	55
Species large when adult	32	Species large when adult	20	Species large when adult	19
Species small when adult	40	Species small when adult	8	Species small when adult	36
Percentage small species	55·5	Percentage small species	28·6	Percentage small species	65·5

Physical conditions in the Middle Zambezi have of course been recently very drastically altered by man, and it is of great interest that a permanent vegetation is already beginning to form in the river below the Kariba Dam. This will probably increase when the dam reaches retention level in 1963/64, and it is quite possible that within the next decade some small species from upland streams within the system will colonize the Middle Zambezi below the dam. The dam has already, within its basin, had the effect of enormously increasing the total fish population of the area (Jackson 1961b).

ANADROMESIS FROM LARGE LAKES

A special aspect of fish migration in African fresh waters is the phenomenon of anadromesis. So far as is known, each of the large African lakes harbours

some species which leave the lake at certain times of the year, the journey often ending in some river or stream far removed from the lake. Later, there is a return of the surviving fish to the parent body of water.

It is a remarkable fact that in every known case the anadromous species are either not endemic to the water concerned or belong to non-endemic genera with closely related species outside the lake. Thus not one member of the endemic species-flocks of Lakes Nyasa, Tanganyika and Victoria, is as yet known to have anadromous habits. Matthes (1961), for example, does not list a single endemic genus as migrating out of Lake Tanganyika to spawn. In Lake Nyasa the anadromous species include *Barilius microlepis* (Gthr.) and *B. microcephalus* (Gthr.), *Barbus johnstoni* Blgr. and *Barbus eurystomis* Keil., and *Labeo mesops* Gthr. In Lake Tanganyika the anadromous species include *Barbus tropidolepis* Blgr. *Auchenoglanis occidentalis* (C. & V.), *Alestes macrophthalmus*, *Citharinus gibbosus* Blgr., *Barilius moorii* Blgr. and *Hydrocyon vittatus*. In Lake Victoria such species include *Barbus altianalis radcliffi* Worth., *Labeo victorianus* Blgr., *Alestes nurse* (Rupp.), *Gnathonemus longibarbis* Hilg., *Clarias mossambicus* and *Tilapia variabilis* Blgr. All these examples are non-endemic or have closely related congeners outside the lake, and all are from old genera, known to have been in existence before the formation of the lakes in their present form.

Whitehead (1959) has suggested that the anadromous habit developed through an extension of the feeding phase in purely riverine species. In my view, however, though it is of course necessary for adequate food for young fish to be available, this is a secondary impulse. The end-point of most African fish migration is a spawning activity whereby the eggs are laid at a place removed from the normal habitat of the adult, anadromesis being no more than a special case where the migration is out of a large lake. Thus in most cases the spawning migration and the anadromous habit are one and the same thing, and an older phenomenon than the formation of any African lake in its present form.

It seems probable, as has been shown above, that spawning migrations have, for one of their main purposes, the placing of the immature fish out of reach of the more ferocious predators such as *Hydrocyon* until they are grown to a size large enough for predation to be minimised or, where this ideal cannot be reached, to be as large as possible before seasonal adverse water conditions in the refuge force them to join the main body. It is significant that most lake species which are known to be anadromous are large, reaching a size in the adult greater than the critical size above which predation risks from *Hydrocyon* are minimal. Considerations of space and food make large fish more open-water living than small species, most of which, other than endemic species-flock members, live and spawn in sheltered lake habitats, and these are less anadromous in habit (for example the Lake Victoria fish mentioned by Whitehead (1959) as known to be anadromous comprise many more species the adults of which exceed 20 cm. in length than those who do not). It is important that food also be available in the refuge, but this I believe to be a secondary consideration. In many cases fish could spawn in their adult habitat without any need for an arduous migration, but if this habitat supports

a large *Lates niloticus* or *Hydrocyon vittatus* population, predation pressure on the young would be too great for the survival of the species.

It is very difficult to escape the further conclusion that even in those lakes where the fierce predators are not present, the anadromous habit is still maintained by the ancestral impulse to spawn where the young are in a refuge. All known anadromous genera were in existence before the formation in its present form of the lake in which they live, so all must have been at one time in contact with the equally ancient genera *Hydrocyon* and *Lates*, and their spawning habits at that time have persisted to the present. The endemic genera (and I include here many of the species now included in the genus *Haplochromis* Hilgendorf, believing that future taxonomic work will require a narrower view of this genus), and such species as the Nyasa *Tilapia* which are not closely related to their congeners, had no such problem. For this reason speciation proceeded apace in those lakes where *Lates* and *Hydrocyon* are absent; the new species were freed from the inhibiting impulse to spawn where the young had a refuge from these fierce predators. Lake Tanganyika admittedly is a case where *Lates* and *Hydrocyon* are present and speciation has yet proceeded, but the factors which make Lake Tanganyika a special case will be discussed in the next section.

PREDATION AND SPECIATION

Worthington, following studies on the Great Lakes, gave it as his opinion (1937, 1940, 1954) that predation by the two genera of voracious predators *Lates* and *Hydrocyon* had important effects on the controlling of speciation, for the reason that a form in an intermediate stage would not be properly adapted to any habitat and might thus find it difficult to survive the impact of predation by these powerful predators. Some controversy has grown up with regard to this theory.

There is at present more evidence in support of the theory than there is against it. First there is the fact (Worthington 1937) that speciation has taken place to a greater extent in those lakes where *Lates* and *Hydrocyon* are absent, with the exception of Lake Tanganyika. Secondly Lowe (1959) supports the case by saying that the particular predators *Lates* and *Hydrocyon* do seem to have had a marked effect on fish, and pointing out a second fact, that Nyasa, without these predators, is the only lake with a genuine species-flock of *Tilapia*. Thirdly she lists a table (p. 17) giving the numbers of *Tilapia* species in lakes with and without these predators, in which three lakes with *Lates* and *Hydrocyon* have eleven species (3·67 species each) between them of which only two (0·67 species each) are endemic, while five lakes without these particular predators have thirteen species of *Tilapia* (2·6 species each) of which no less than ten (2·0 species each) are endemic. Fourthly Jackson (1961a) gives data regarding the feeding habits of *Hydrocyon vittatus* and gives evidence to show that in this water (the Middle Zambezi) *Hydrocyon* has a very marked effect upon the other fishes. Finally there is the evidence in the present paper, which is in support of this theory.

In contrast, the case against the theory that these predators have influenced speciation has had little evidence brought forward to support it, but has

remained largely speculative. Mayr (1942) believed that the age and size of the lakes were vastly more important than the presence of these predators, retabling Worthington's (1937) table to bring out the fact that some lakes are older than others. Mayr brings forward no other evidence. A paper by Fryer & Iles (1955) contributes even less evidence as it disagrees with Worthington solely on the grounds that, while *Lates* and *Hydrocyon* are admittedly absent, there are fishes in Lake Nyasa which prey wholly or partly on other fish, a fact which was already well known (Worthington 1933, Bertram *et al.* 1942, Trewavas 1949, Lowe 1952). Fryer & Iles make the further remarkable statement that " it has been observed that almost any fish in the lake, whether carnivore or herbivore, will take the eggs or fry of other fishes whenever the opportunity to do so arises ". This assertion is improbable in the extreme, since it has long been known (Trewavas 1949) that the Nyasa endemics are for the most part minutely specialized to special feeding habits on definite animal or vegetable foods to which their dentition is characteristically adapted. The only conditions under which these specialized forms can be visualized as eating eggs even accidentally are if kept half starved in an aquarium, or perhaps during capture by a seine net. It is therefore scarcely surprising that no evidence whatever has ever been published to support this assertion. A later paper by Fryer (1959 a) emphasizes the specialized feeding habits of littoral fish, and lists only a single case of eggs being eaten among many careful records. Contrary to a later opinion (Fryer 1959 b, p. 445), that " every available niche appears to have been filled ", there is as yet no evidence of the egg-eating niche having been filled. Future work on Lake Nyasa, however, might reveal a species which specializes in egg-eating ; with such an unusual habit as scale-eating known from here (Bertram *et al.* 1942, Trewavas 1947) existence of a specialized egg-eater is possible, but such a habit is not by any means universal.

Fryer (1959 a) believes that the predatory fish of Nyasa have encouraged speciation among rocky shore forms, believing that, by preying on the most abundant, the predators there allow newer and therefore less numerous forms to multiply. He assumes that " the most abundant species will form the major portion of the diet of predators " (p. 272), but admits a certain variation in predation, due to differing habits of the predators. Thus he assumes (p. 226) " species of *Rhamphochromis* occur in general at the fringe of the rocky shore and must therefore compete only to a small extent with species living close inshore ". Again, " species such as *Bagrus meridionalis* and the clariids which visit the shore differ markedly in behaviour from the piscivorous cichlids and therefore probably tend to encounter different fishes ". Unfortunately, while the food of non-predatory fish has been carefully studied in this paper, very little data on the food components of the predatory species is given, and also no evidence as to whether there is any selection of prey, whether the predation impact falls most heavily on any one size-group or section of the population, or whether any predator is relatively more voracious or otherwise more significant in its impact than another.

While the present paper is concerned specifically with the genera *Lates* and especially *Hydrocyon*, it may be said in passing that the assumption that

the most abundant species will furnish the major part of the predators' diet in the complex lake Nyasa seems unduly large and insufficiently comprehensive when discussing the effect of predation on speciation, on the present scanty evidence. There are many factors to be considered, including those of relative size of predator and prey, use of evasive mechanisms such as scattering or taking cover, or the use of shallow water by small fish, seasonal movements and migrations, such as those of the predatory *Barilius* out of the lake into rivers (Lowe 1952, Jackson *et al.* 1961) when their impact on the wholly lacustrine population is reduced by the extent of their absence, and perhaps most important, the question of the voracity of the various predators.

The question of size is likely to be important. The majority of Nyasa endemics are of small size. Excluding an unspecified number of *Rhamphochromis* which in any case only fringe on the rocky shore (see above) and can thus be safely left out of the discussion, Fryer (1959 a) lists thirty-one species as habitually occurring there in Lake Nyasa. Of these only ten exceed a length of 18–20 cm. when adult, of which some, e.g. *Haplochromis kiwinge* Ahl., are normally very much smaller as they spend their adult life in another habitat, while others, e.g. *Mastacembalus shiranus* Gthr. and *Bathyclarias worthingtoni* Jackson, lead a very secretive life under stones and will probably prove unlikely to form a great part of any predator's diet. Thus the great bulk of the rocky shore fish are small in size when adult, especially those exposed to predation, and this seems to argue that the Nyasa rocky shore predators are too mild to have had much effect upon the numerous endemic species continually living there, as it has been shown that the impact of predation by *Hydrocyon* is upon small fishes, and it seems reasonable, though evidence is absent, to assume that the same applies in Nyasa with its infinitely milder predators. Furthermore it is known that in the absence of predators, for example if they should be artificially removed from an environment, other fishes will increase rapidly in numbers but individuals tend to diminish in size (see, e.g., Rounsefell & Everhart (1953), pp. 47, 366).

The main point at issue, however, is Worthington's thesis that speciation has been affected by the voracious predators *Hydrocyon* and *Lates*. It may be, as Fryer has argued (1959 a, b), that the milder Nyasa predators have encouraged speciation by bearing against all the most abundant species (if this is indeed so), thus reducing interspecific competition by reducing their numbers, and promoting speciation by encouraging the isolation of populations within the lake. But from accepting this secondary effect to accepting the contention that absence of the active *Hydrocyon* and *Lates* has had nothing to do with the great speciation which has occurred in Nyasa is a very long step, greater than it is possible to take in the light of our present knowledge, most of which favours the opposite view.

Nyasa's sister lake, Tanganyika, is of great interest in being also a rift lake in which speciation, especially among cichlids, has gone on but which harbours the two fierce predators in question. Physically the two lakes are similar though Tanganyika is older, and the fact that speciation has occurred extensively in spite of the presence of these predators has been used in refutation of Worthington's argument.

In fact, however, there are a number of ecological factors in the life-history of both *Lates* species and *Hydrocyon vittatus* in Lake Tanganyika which have not yet been considered. The species of *Lates* present are all pelagic and open-water living when adult, and feed very largely indeed on the pelagic clupeids *Limnothrissa miodon* (Blgr) and *Stolothrissa tanganicae* Regan, and on the small predators (*Bathybates*, etc.) which are themselves preying upon these clupeids. It is usual to find stomachs of large *Lates* 120 cm. or more in length packed with clupeids 10 cm. or less in length. Thus the impact of predation of adult *Lates* in Lake Tanganyika is almost exclusively on a few open-water species and very little towards those littoral species which form the great majority of the lake's endemic species. This is in contrast to the habit of the Nile Perch, *Lates niloticus* (L.), which according to Kenchington (1939) feeds on a variety of species of *Hydrocyon*, *Alestes*, *Labeo* and *Barbus*.

There are several ecological factors in the case of *Hydrocyon vittatus* in Lake Tanganyika, too, which must be taken into account. This species has an annual spawning migration up large rivers. This means that its impact of predation on endemic species is in the first place reduced annually by the extent of the absence of adult predators on the spawning run. Secondly the tiger-fish is by no means abundant in Lake Tanganyika ; it is, in fact, one of the relatively scarcer fish present. The main reason for this is undoubtedly the limiting factor of the rarity of suitable large rivers, without waterfalls or other barriers near the entrance to the lake, for use in spawning. In the whole of southern Lake Tanganyika there is only one river used by *H. vittatus* for spawning migrations ; that is, the Lufubu. Round the whole lake there are the Malagarasi and the Ruzizi, and a few others. Thus the impact of predation of this species in Tanganyika is lessened also because of its comparative scarcity in the lake.

It can thus be seen that, in general, predation pressure by *Lates* and *Hydrocyon* in Lake Tanganyika is very considerably less on most species than might be assumed merely on the knowledge that both genera are present in the lake. If one adds to this the facts of the greater age of the lake and the greater number of endemic genera than, say, Lake Nyasa, there is very little indeed in a consideration of Lake Tanganyika to militate against the theory that predation has influenced speciation.

CONCLUSIONS

This paper deals with one facet of the whole problem of predator/prey relationships, a problem far too large to be discussed here, though it is perhaps possible that the concept of refuge for young fish being a primary factor in spawning migrations might be found to extend to several other fishes with demersal eggs, such as anadromous species and many which come to shallow littoral areas to spawn, in contrast with catadromous species which have pelagic eggs and larvae.

A main conclusion of the present paper is that *Hydrocyon vittatus* has a marked impact upon the lives of other fish and that this impact is mainly on those fish which are small in size. As a result cover is used a great deal by

small fish to escape this predation, and vegetation and shallow water is also used as a refuge by the young of larger fishes in which to spend as much of their early lives as possible, until the danger of predation by the tiger-fish is minimized. The amount of time in the refuge is often limited by physical conditions, especially the seasonal abundance of flood-water which submerges more vegetation than is the case in the dry season ; such refuges must of course be abandoned when the flood-water recedes. Thus, as the physical conditions vary, so do the details of cover and the amount of time spent in the refuge vary from place to place. The other essential that a refuge must have is sufficient food to support the population of small fish. Sooner or later, as Elton (1939) has remarked, an animal must come out of its refuge in order to live, and, if not accelerated by adverse physical conditions, the time of emergence from the refuge (such as in the case of *Tilapia macrochir* in Lake Mweru where physical conditions do not limit the animal's stay in the refuge) seems to be significantly correlated, by the maximum size to which the fish has grown in the time, to the minimum size at which predation pressure by *Hydrocyon vittatus* is no longer effective.

Cases are known (e.g. in the Bangweulu swamps) of fish making regular movements to avoid water deoxygenated in the dry season or to re-inhabit water freshly oxygenated by flooding at the start of the rains and it is possible that in some cases the factor of adequate oxygen requirements for demersal eggs and young may motivate a spawning migration : but in the African spawning migrations mentioned above, oxygen lack in the original habitat is in no case known to be a limiting factor and it is believed that two factors affecting the well-being of the young, adequacy of cover and sufficiency of food, are the main causes of the extensive and often arduous spawning migrations undertaken annually by so many African fishes at the season when these two factors are likely to be at their most favourable. The factor of refuge from predation seems to be much the most important of the two, since in waters inhabited by *Hydrocyon vittatus* (probably also where *Lates niloticus* and its subspecies occur), adequate feeding grounds for young fishes may often be found without the necessity for extensive migrations but where, however, the young are exposed to predation. It is believed further that the necessity for making these extensive migrations each year, involving always a complex change from one definite habitat to another, equally definite, has tended to limit speciation. Speciation has, therefore, occurred mainly in those genera in lakes, and species well removed from congeneric species outside, which have never known predation pressure from these ferocious predators. The conclusion follows therefore that Worthington is correct in his theory that predation by *Lates* and *Hydrocyon* has had a marked retarding influence on speciation of African fishes. As this author puts it (1954) : " The contention is that, where predators are continually on the prowl, the lesser forms, adapted to their particular ecological niches, can depart from them to colonize new microenvironments or to breed with their neighbours only on pain of death ". The fact that an ecological niche is where cover exists for young fish is a detail of the same concept ; a young or small fish can leave its refuge, where *Hydrocyon* prowls, only on pain of death.

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A NEW SPECIES OF *SABELLACHERES* (CRUSTACEA : COPEPODA) PARASITIC ON THE FAN WORM *EUDISTYLIA POLYMORPHA* (JOHNSON)

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(With 14 figures in the text)

The female and nauplius of *Sabellacheres dalesi* sp. n. are described and figured. A key to the genera and species of the Gastrodelphyidae is given.

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INTRODUCTION

The remarkable copepod described below was discovered by Dr R. P. Dales during his researches into the physiology of fan worms. It gives me great pleasure to name the species after him.

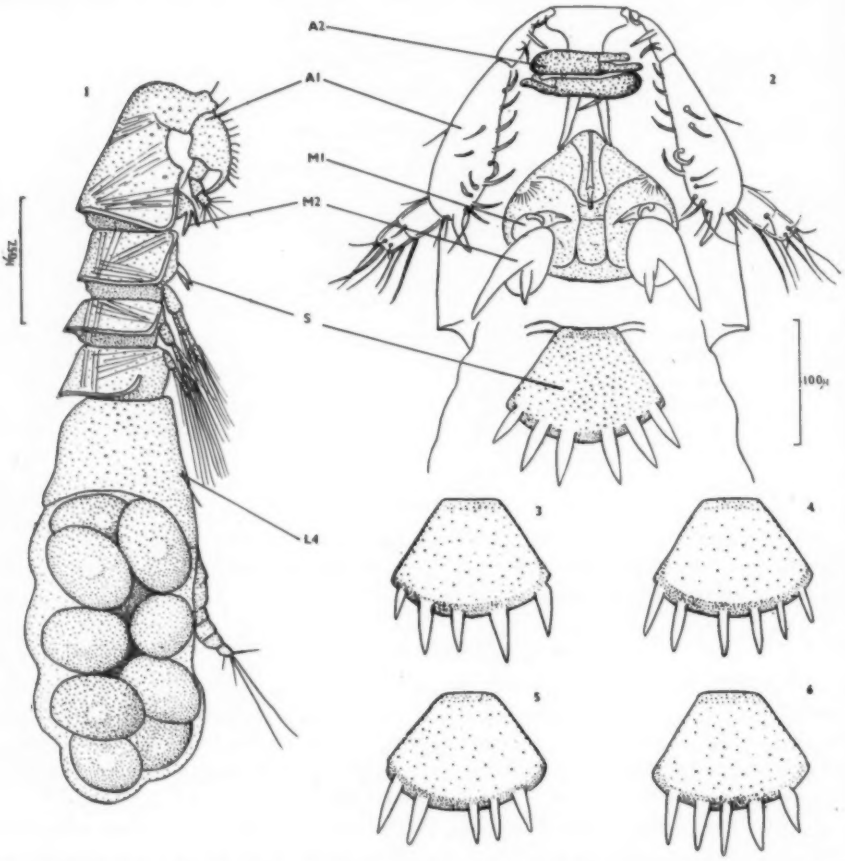
SABELLACHERES DALESI sp. n.

Female. The general form of the body is shown in Fig. 1. The total length including the brood sac is about 1·4 mm. There is a distinct cephalon bearing a pair of large antennules antero-laterally. The rostrum forms the antero-ventral part of the cephalon and can be separated as a distinct sclerite prolonged posteriorly in the form of two large spines (Fig. 9).

The antennule consists of five podomeres, the two basal ones being enlarged and flattened. Some of the setae on these basal podomeres have the outer layer of the podomere cuticle continued over the setal surfaces, so that a curious flanged appearance results when viewed by transmitted light. The second podomere is prolonged in the form of a large spine distally (Fig. 8). Thickenings of the integument near the base of this spine give the appearance of a line across the base, but the spine is not articulated. When viewed from the ventral surface the enlarged second podomere obscures the third podomere (Fig. 2), but this is easily seen in lateral view (Figs. 1 & 8). The three distal podomeres are cylindrical in form.

The antennae lie crosswise between the bases of the antennules (Fig. 2) ; this is clearly an adaptation to grip the filaments of the host crown. There

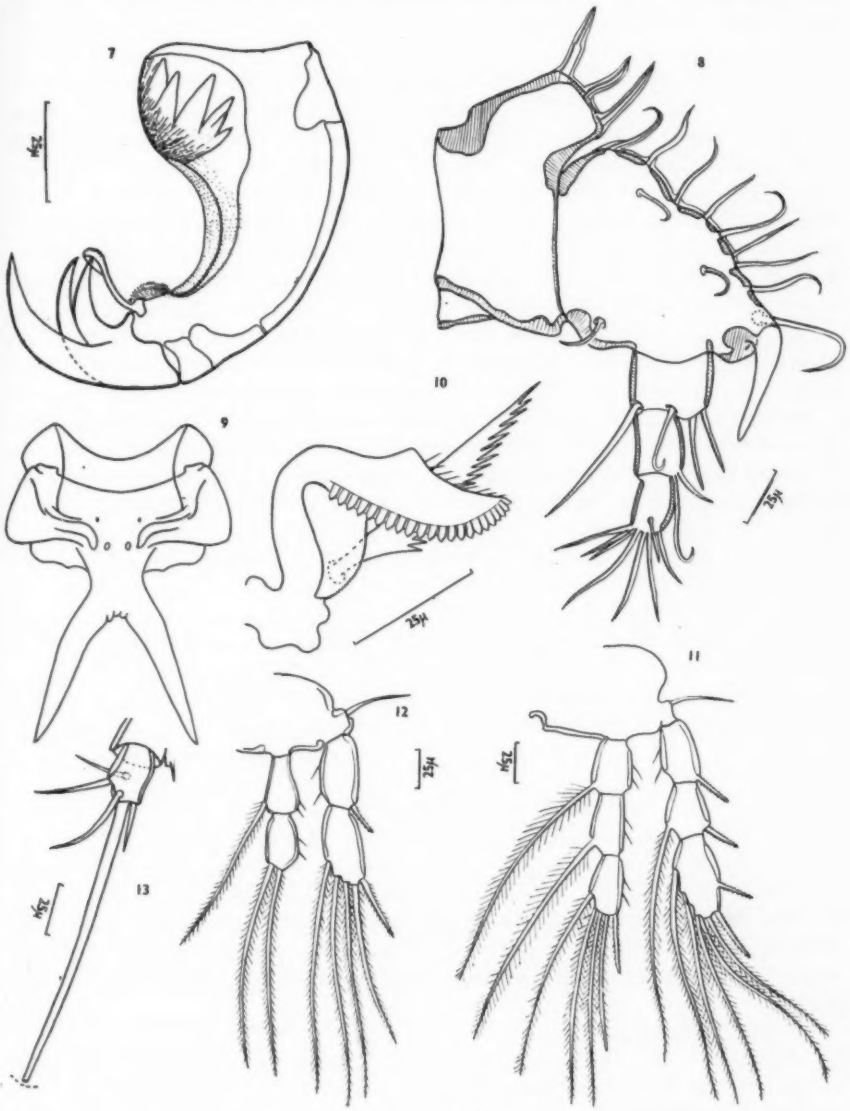
are four podomeres forming each antenna ; the last one bears a plate with a strongly serrate edge near the base and three heavy claws at the tip. A curious spoon-shaped seta arises near the base of the most proximal of the three claws and caps its tip (Fig. 7). At the base of the spoon-shaped seta is a pad bearing minute spinules.



Figs. 1–6—*Sabellacheres dalesi* sp. n. 1, lateral view of female. 2, ventral view of the anterior end of female. A1—antennule, A2—antenna, M1—first maxilla, M2—second maxilla, S—sternal plate, L4—fourth leg. 3–6, variations in the spines on the sternal plate.

The mandible (Fig. 10) has its main body bent into the form of an S. The basal portion is expanded into a thin flange with a very finely milled edge. A large spine arises from the basal portion and projects diagonally forwards towards the mouth. The medial edge of this spine bears about 18 large serrations. The main body of the mandible continues obliquely in a posterior direction in the form of a tongue-shaped process bearing about twenty-two distinct teeth along one border and a graduated series of small hairs along

the other. There is a large triangular projection near the middle of the border bearing the hairs. In Fig. 10 the toothed process is shown as being flat, but when in its normal state inside the mouth the distal tip curves ventrally.



Figs. 7–13—*Sabellacheres dalesi* sp. n. 7, apex of antenna. 8, left antennule, medial view. 9, rostrum separated from the rest of the exoskeleton. 10, left mandible, dorsal view, somewhat flattened. 11, first swimming leg. 12, third swimming leg. 13, right caudal ramus, ventral view.

The first maxilla bears two medially directed processes and a longer ventrally directed spine.

The second maxilla is larger than the first and is prolonged in the form of two posteriorly directed spines, the lateral one being much larger than the medial one.

No maxilliped was found.

Behind the cephalon are three apparent segments, the first of which bears two distinct structures. The anterior structure takes the form of a plate bearing five or six stout spines on the posterior border. There is some variation in the size of these spines, and they do not always form an even series (Figs. 3–6). The homology of this plate is uncertain, but there are distinct sternal articulations at the antero-lateral corners, and large muscles run to various parts of the plate. In Figs. 1 and 2 the noncommital label ' sternal plate ' has been applied. In List's (1890) descriptions of *Gastrodelphys clausi* and *G. myxicolae* the term ' Bauchwirbelkörper ' is applied to this structure.

The second structure on the first apparent free segment is the first pair of swimming legs (Fig. 11). The second and third apparent segments each bear a pair of swimming legs. The second swimming legs are similar in all respects to the first except that the terminal podomere of the exopodite bears an extra plumose seta. The third swimming legs have only two podomeres in both the exopodite and the endopodite (Fig. 12). The last or 4th leg is represented by a small papilla bearing a single seta.

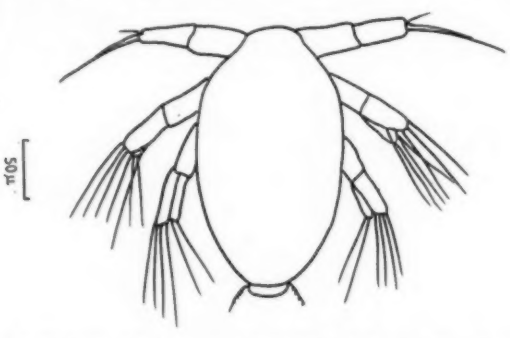


Fig. 14—*Sabellacheres dalesi* sp. n. Newly hatched nauplius, dorsal view.

The brood sac projects dorsally beyond the tip of the abdomen, which is small and consists of four segments. Each caudal ramus (Fig. 13) bears five setae, one of which reaches a length of 280 μ while the others are all much shorter.

Male. Unknown.

Nauplius. The newly hatched nauplius is shown in Fig. 14. The total length of the body, excluding setae is about 220 μ. The antennules are uniramous with one long and one short terminal seta. The antennae are biramous with five setae on the exopodite and two setae on the endopodite ; the mandibles are similar in structure but have only four setae on the exopodite. The furcal setae are feathered along their medial borders.

Occurrence. Five females were found by Dr R. P. Dales on the branchial crowns of *Eudistylia polymorpha* Johnson (Polychaeta, Sabellidae) which had been sent to him from a collecting station three miles North of Point Dume at the western end of Zuma Beach, near Los Angeles, California. The worms were collected from between rocks in water varying in depth from 25 to 50 feet, in mid August 1959.

Dr Dales noted that the females were capable of active swimming and could detach themselves from the host crown, swim around for a short while, and then reattach themselves.

DISCUSSION

The species described above is similar in many respects to *Vermiclavella elongata* described by Markewitsch (1940) from *Myxicola*, but it is a much smaller species (total length 1·4 mm. compared with 4·6 mm. in *V. elongata*), and both the rami of the third swimming leg have only two podomeres compared with three in *V. elongata*.

The two species of *Gastrodelphys* described by List (1890) have the swimming legs greatly reduced and are presumably incapable of swimming. It seems probable that here we have a series of stages showing reduction of locomotory activity associated with the adoption of a parasitic mode of life. If we regard all the forms as belonging to one genus some problems of nomenclature become apparent. *Vermiclavella* Markewitsch 1940 would become a synonym of *Gastrodelphys* Graeffe 1883. The problem is complicated by the fact that Sars (1862) gave a brief description of a copepod parasitic on *Myxicola* and gave it the name *Sabellacheres gracilis*. A comparison of Sars's description with the figures given by Markewitsch (1940) indicates that they were looking at the same species. If all the species are congeneric the correct name would be *Sabellacheres* Sars. It seems preferable at the moment to retain *Gastrodelphys* for those species with greatly reduced swimming legs, so that the hitherto described species of the family Gastrodelphyidae can be separated as in the following key.

FAMILY GASTRODELPHYIDAE LIST 1890

The diagnosis of this family will have to be extended from that given by List to include forms with well-developed swimming legs. Antennules with five podomeres, the first two of which are flattened and enlarged. Antennae with four podomeres the last of which bears three large claws. First apparent thoracic segment bearing a sternal plate with posteriorly directed spines. Brood sac dorsal, projecting above the abdomen. Parasitic on annelids.

1 (4). Three pairs of swimming legs well developed, with at least two podomeres in both rami ..... *Sabellacheres* Sars 1862.

2 (3). Third swimming legs widely separated from the first two pairs and with three podomeres in both rami. Large species, up to 5 mm. long, parasitic on *Myxicola* ..... *S. gracilis* Sars 1862 (syn. *Vermiclavella elongata* Markewitsch 1940).

3 (2). Third swimming legs not widely separated from first two pairs and with only two podomeres in exopod and endopod. Length, including egg sac, 1·4 mm. Parasitic on *Eudistylia*. *S. dalesi* sp. n.

4 (1) Swimming legs reduced. Endopods of single podomere or absent ..... *Gastrodelphys* Graeffe 1883.

5 (6). Endopods present on first two pairs of legs. Abdomen with three segments. Parasitic on *Bispira volutacornis* ..... *G. clausi* Graeffe 1883.

6 (5). Endopods absent. Abdomen with one segment. On *Myxicola* ..... *G. myxicolae* List 1890.

ACKNOWLEDGMENT

I am greatly indebted to Dr Paul Illg for his helpful comments on my preliminary draft of this paper.

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FRUIT-BATS FROM THE FEDERATION OF MALAYA

BY

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[Accepted 13th December 1960]

(With 1 figure in the text)

An account is given of hitherto poorly known Malayan Megachiroptera recently received at the British Museum (Natural History) from the Institute for Medical Research, Kuala Lumpur. Variation in *Cynopterus brachyotis* from the south-east Asian mainland is studied and a hitherto unknown Malayan race described ; two genera, *Dyacopterus* and *Aethalops*, are recorded for the first time from the Asiatic mainland and the taxonomy of a number of species of Malaysian Megachiroptera discussed.

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INTRODUCTION

The collections of the British Museum (Natural History) are rich in Malayan mammals, especially since the accessions of the type specimens once in the Raffles Museum, Singapore (Gibson-Hill, (1949)) and of the Robinson collection (Hill, (1960)). However, some species and even genera of Malaysian bats, especially Megachiroptera, have been represented for many years in London by one or two specimens or by a small series. It is therefore a pleasure to record that through the courtesy of Professor J. L. Harrison, now of Nanyang University, Singapore, the British Museum (Natural History) has recently received a large collection of Malayan bats from the Institute for Medical Research, Kuala Lumpur. Collected for the most part in the States of Selangor and Pahang by a member of the Institute staff, Mr Lim Boo Liat, the collection is especially noteworthy for its extensive series of Microchiroptera and for its richly varied representation of Megachiroptera. Mr Lim Boo Liat has in fact secured one or more specimens of every megachiropteran genus hitherto listed from Malaya, excepting *Pteropus*, and has also obtained two genera new to the Asiatic mainland. The following notes derive from the examination of the less common and more interesting fruit-bats in the collection and their comparison with the collections of the British Museum (Natural History).

Specimens are listed under their British Museum (Natural History) registration numbers. Measurements are in millimetres : those of series of specimens are expressed as the minimum and maximum of the series, followed by the arithmetic mean in parentheses. No detailed synonymies are given, except where these have been created or nomenclatorial changes made, as Chasen

(1940) and Ellerman & Morrison-Scott (1955) adequately list the synonymies of Malaysian mammals.

SYSTEMATIC SECTION

CYNOPTERUS BRACHYOTIS BRACHYOTIS (S. Müller)

1838 *Pachysoma brachyotis* S. Müller, Tijdschr. nat. geschied. physiol. **5**, pt. 1 : 146. Borneo.

Perak : ♀♀ 60.674–676 Pulau Pangkor.

Selangor : ♂♂ 60.623–636, ♀♀ 60.637–639, 60.650–663 Bukit Lagong Forest Reserves, Kepong. ♀ 60.673 Sungei Buloh Leper Settlement, Kepong. ♀ 60.670 Kuang, Sungei Buloh, Kepong. ♀♀ 60.677–678 Ulu Langat Forest Reserves, Kajang. ♂ 60.671 Lake Garden, Kuala Lumpur. ♂♂ 60.614–617, ♀♀ 60.618–622 Ampang village, Kuala Lumpur. ♂♂ 60.666–667, ♀♀ 60.611–613, 60.668 4½ miles Kapor Road, Klang.

Negri Sembilan : ♂♂ 60.640–641, ♀♀ 60.642–649, 60.664–665 Rifle Range Port Dickson. ♀ 60.672 Military Camp, Port Dickson. ♂ 60.669 Telok Pelandok, Port Dickson.

One specimen, ♂ 60.692, is said to have come from Mount Brinchang, Cameron Highlands, Pahang, but more probably originated from Bukit Lagong Forest Reserves, Kepong, Selangor (see below).

All specimens in alcohol.

Andersen (1912) thought that two subspecies of *Cynopterus brachyotis* occurred together in the Malay Peninsula and Sumatra. This long series supports the view of Chasen (1940) that the southern part of the Malay Peninsula is inhabited by a brightly coloured race of *C. brachyotis* with small ears which in the northern part of the Peninsula is replaced by a larger, somewhat darker race with larger ears. These specimens represent the southern race *C. b. brachyotis* : fifty-seven adults have a forearm length of 57·0–68·0 (61·5) and ear length of 15·0–18·5 (17·0). As Chasen points out, the maximum forearm length occurs but rarely, and of this series only eleven specimens have the forearm 64·0 or more in length while in only two examples does the length of the forearm reach or exceed 65·0. Twenty specimens of *C. b. angulatus* Miller, the larger northern race, from Siam, Tenasserim and Burma have corresponding measurements (taken for the most part from dry skins : ear lengths are those recorded by the collectors) of : length of forearm 66·5–72·0 (69·0) and length of ear 19·0–22·0 (20·0). The forearm and ear lengths of the two races are compared in the scatter diagram (Fig. 1).

The exact zone of intergradation between the races is uncertain. Chasen (1940) considered *C. b. brachyotis* to extend as far north as Penang Island and Kedah but specimens in the collection of the British Museum (Natural History) from South Perak (8.2.5.10, 8.2.5.12–14) have a forearm length of 68·5–70·0 (69·0) and ear length of 19·0–20·0 (20·0), while others from Batang Padang, South Perak (8.2.5.8) and Ulu Ijok (34.7.18.16) measure 69·5, 70·5 and 18·0, 19·0 respectively. These specimens show that *C. b. angulatus* extends further south than was thought by Chasen. Intergradation must take place over a wide area : a series from Kuala Kangsar, northern Perak, described below, is smaller and approaches *C. b. brachyotis*.

One female specimen, 60.691, labelled Bukit Lagong Forest Reserves, Kepong, Selangor, does not agree in size and colour with *C. b. brachyotis* and appears to belong to the series from Mount Brinchang, Cameron Highlands, Pahang, described below.

CYNOPTERUS BRACHYOTIS ALTITUDINIS subsp. nov.

Type ; B.M.60.702. Adult ♂. Mount Brinchang, Cameron Highlands, Pahang, Federation of Malaya, 5,500 ft. Collected by Mr Lim Boo Liat on 12th June, 1959 and presented by the Institute for Medical Research, Kuala Lumpur. Skinned from alcohol in June, 1960. Skull in good condition.

Other material : ♂♂ 60.693, 60.694 (skull extracted), 60.704–706, ♀♀ 60.695–701, 60.703 (skinned from alcohol, June, 1960, with skull), 60.707–710 Mount Brinchang, Cameron Highlands, Pahang, 5,500–6,600 ft.

(?) ♂♂ 60.679–684, ♀♀ 60.685–690 Operation Kerbau, Kuala Kangsar, Perak (see below).

One specimen, ♀ 60.691, is said to have come from Bukit Lagong Forest Reserves, Kepong, Selangor, but more probably originated from Mount Brinchang, Cameron Highlands, Pahang (see below).

All specimens in alcohol unless stated.

Diagnosis. A montane race closely related to *Cynopterus brachyotis brachyotis* and *C. b. angulatus* but with markedly darker overall coloration than either of these races. The forearm of *C. b. altitudinis* averages longer than that of *C. b. brachyotis* but is considerably shorter than that of *C. b. angulatus*. The ears of the new race are much longer than those of *C. b. brachyotis* and in this respect it approaches *C. b. angulatus*.

Description. The dorsal surface is dark brown, the hairs of the back dark grey brown at the base with dark brown tips. The general dorsal colour corresponds closely with the Munsell colour 10.0 YR 3/2. The shoulders are tinged with dark grey, while the dorsal surface of the head is the same colour as the back. Ventrally, *C. b. altitudinis* is paler, the ventral colour being grey brown and corresponding to Munsell 2·5 Y 6/2. A minority of specimens have browner underparts and are nearer to *C. b. brachyotis* and *C. b. angulatus* in ventral colour. Shoulder and throat patches are occasionally represented by a few brightly yellowish or orange hairs but otherwise are absent. The ears are conspicuously edged with white. The pelage of *C. b. altitudinis* is dense and rather long, both dorsally and ventrally. The darker coloration of *C. b. altitudinis* differs markedly from *C. b. brachyotis*, in which the dorsal and ventral surfaces are much browner, corresponding to Munsell 10·0 YR 5/8 and 10·0 YR 6/6 respectively. *Cynopterus brachyotis altitudinis* differs less sharply in colour from *C. b. angulatus*, a race rather darker than *C. b. brachyotis* having the dorsal and ventral surfaces approximating to Munsell 10·0 YR 5/4 and 2·5 Y 6/4.

Measurements. Dimensions of the type specimen and (in parentheses) a second male specimen (60.694) : length of forearm 64.0 (66·5), length of ear 19·5 (20·0), greatest length of skull 30·2 (29·2), condylobasal length 28·7 (28·5),

palatal length 15·3 (14·9), orbit-nares 13·0 (12·9), zygomatic width 18·8 (by extrapolation) (20·1), interorbital width 5·3 (5·8), postorbital width 6·0 (6·2), braincase width 13·0 (12·9), m^1–m^1 8·8 (8·7), c–c 5·9 (6·0), c–m^1 9·7 (9·5), c–m_2 11·1 (10·9) (all tooth measurements made at the alveoli). The length of the forearm in sixteen specimens is 60·5–67·5 (64·0) and of the ear 18·5–20·5 (19·5).

A male specimen, 60.692, labelled Mount Brinchang, Cameron Highlands, Pahang, differs sharply from the remainder of those listed in its bright brown dorsal colour, brown ventral colour, less conspicuous edging to the ears and well marked orange throat band. There is among the series listed above as *C. b. brachyotis* a female specimen, 60.691, labelled Bukit Lagong Forest Reserves, Kepong, Selangor which exactly matches the Mount Brinchang series in colour. The two specimens have forearm and ear lengths of 65·0, 66·0 and 18·0, 19·5 respectively. Apart from these two specimens both series are entirely consistent in colour, and this, with the difference in ear length, points to an error in labelling. The collection was re-labelled before despatch to London and it is quite possible such an error has occurred.

Specimens labelled " Operation Kerbau, Kuala Kangsar, Perak " come from the neighbourhood of Gunong Kerbau, near the Perak-Kelantan boundary. No altitudes have recorded for this series. These specimens cannot be referred definitively either to *C. b. brachyotis* or to *C. b. altitudinis*. In dorsal colour they range from specimens only slightly paler than those from Mount Brinchang to examples with more brightly ochraceous brown backs only very little darker than those from Negri Sembilan and Selangor. Similarly, grey brown underparts in the darker examples give way to browner underparts in the more brightly coloured specimens. They average slightly smaller than the series from Mount Brinchang, but larger than *C. b. brachyotis*. The length of the forearm in a series of eleven specimens is 61·0–66·0 (63·0) and of the ear 17·0–19·0 (18·0). The forearm and ear lengths of *C. b. brachyotis*, *C. b. angulatus*, *C. b. altitudinis* and the series of specimens from Kuala Kangsar are compared in the scatter diagram (Fig. 1).

The majority of the specimens from Mount Brinchang, Cameron Highlands, Pahang, were collected in June, 1959. Others were collected during January and April, 1959 and February, 1960. The series from Kuala Kangsar, Perak was obtained in October, 1959. None of the material has been in alcohol for more than eighteen months at the time of examination. Initially, some reluctance was felt in proposing a new subspecific name based partially on colour for specimens which had been immersed for a time in alcohol but Mr Lim Boo Liat informs me (*in litt.*) that in his recollection *Cynopterus* from Mount Brinchang were very much darker than those he collected in the lowlands of Selangor and Negri Sembilan.

CYNOPTERUS HORSFIELDI MINOR (Lyon)

1908 *Niadius minor* Lyon, Proc. U.S. Nat. Mus. **34** : 665. Confluence of Gasip and Siak Rivers, eastern Sumatra.

1909 *Cynopterus* (*Niadius*) *harpax* Thomas and Wroughton, Ann. Mag. nat. Hist. (8) **3** : 437 (preliminary notice), J. Fed. Mal. St. Mus. **4** : 108. Semangko Pass, Selangor-Pahang boundary 3,000 ft.

1912 *Cynopterus horsfieldi lyoni* Andersen, Cat. Chirop. Brit. Mus. **1**. Megachiroptera, 827 (substitute for *Niadius minor* Lyon nec *Cynopterus* (*Cynonycteris*) *minor*, Trouessart, 1878).

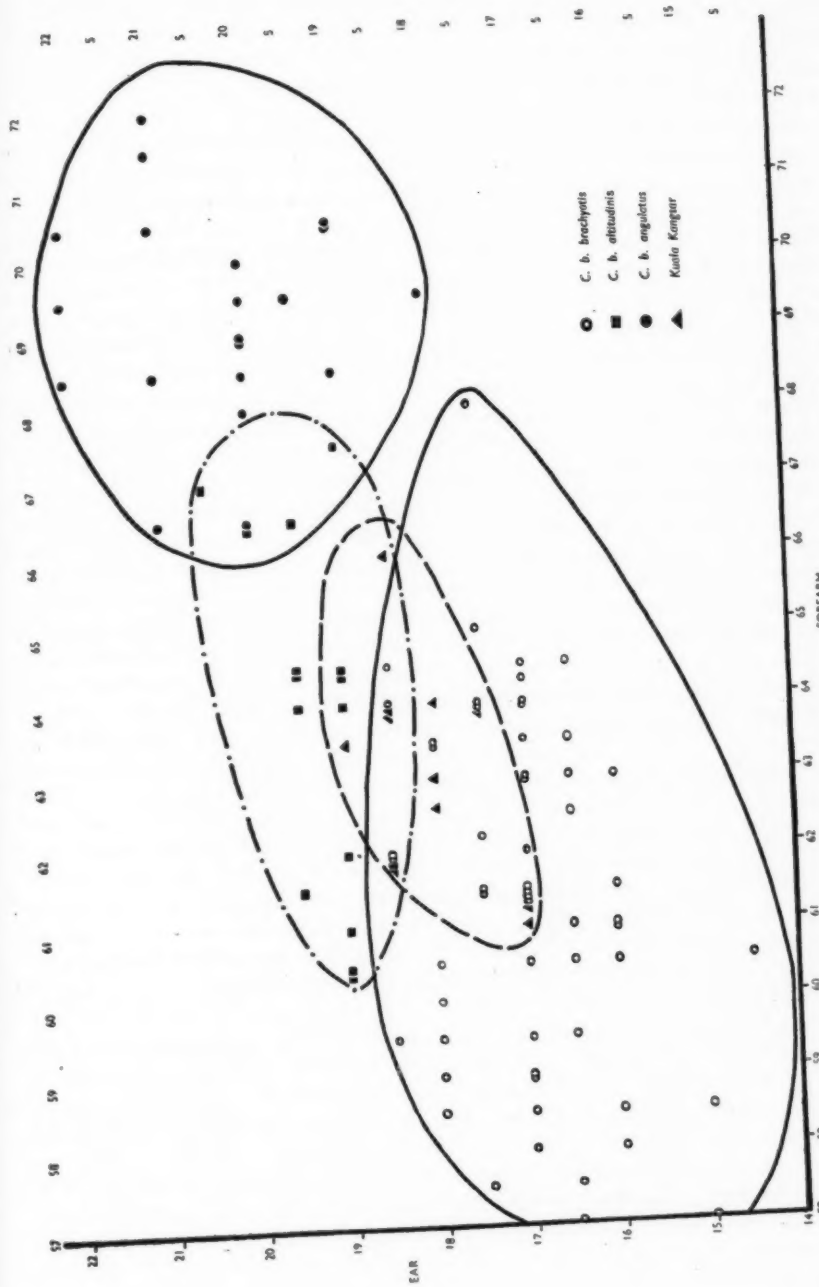

Fig. 1.—Comparison of forearm and ear length of *Cynopterus brachyotis* from south-east Asia.

Selangor : ♂♂ 60.711 (skull extracted), 60.712, ♀♀ 60.713, 60.714 (skull extracted) Ulu Langat Forest Reserves, Kajang. ♂♂ 60.715, 60.721–723 (skulls extracted), ♀♀ 60.716–720, 60.724 (skull extracted), 60.725–730 Bukit Lagong Forest Reserves, Kepong.

All specimens in alcohol.

Malayan *Cynopterus horsfieldi* has hitherto been unrepresented in the collections of the British Museum (Natural History). This series agrees closely in size and appearance with the Sumatran subspecies *C. horsfieldi minor* and is referred to that race. The length of the forearm in thirteen Malayan examples is 70·0–78·0 (73·5). Cranial measurements of Sumatran and Malayan specimens are compared in Table 1.

Cynopterus harpax Thomas and Wroughton is represented in London only by the type specimen, and no further examples appear to have been recorded since Robinson and Kloss collected the original series of five in 1908. Of these, Thomas and Wroughton examined only one, the type specimen, 8.7.20.7, an adult male, not a subadult as stated by Andersen (1912). Thomas and Wroughton in the original description of *C. harpax* seem not to have made a direct comparison with *C. horsfieldi minor* but refer exclusively to its description by Lyon. At the time Thomas and Wroughton prepared their description, three specimens of *C. horsfieldi minor* existed in the collections of the British Museum (Natural History). These, 79.6.28.1 and 79.7.2.4–5, do not appear to have been available to these authors : the skulls in fact have been labelled by Andersen. It is most likely that until Andersen worked upon this material during the preparation of the Catalogue of Chiroptera, these specimens remained labelled *Cynopterus marginatus*, the name applied to them at accession in 1879 and thus were overlooked by Thomas and Wroughton.

Thomas and Wroughton used as the principal character of their definition of *C. harpax* : " Teeth of the same essential structure as in the other two forms of *Niadius*, with the same definite central cusp on p_4 and m_1, but the teeth throughout are narrower, less squared, and the lower ones are narrower posteriorly than anteriorly . . . ". Additionally, the interorbital region was stated to be narrower and the toothrow shorter than in *C. horsfieldi minor*. The other form of *Niadius* referred to, is, of course, *C. horsfieldi princeps*, from Nias Island, west Sumatra, a much larger form. The characters of the teeth of *C. harpax* as defined by Thomas and Wroughton are amplified by Andersen (1912) who says that the posterior tapering of the lower teeth is most marked in the third and fourth premolars and less so in the first molar ; he adds that the third and fourth upper premolars are " distinctly less broadened posteriorly than in the related species ". These attributes of the teeth prove not wholly reliable when a series of *C. horsfieldi minor* is examined. Individuals can be found in which the third and fourth lower premolars and the first lower molar are noticeably narrower posteriorly than anteriorly : equally, there are individuals in which these teeth show little posterior tapering or are square in surface outline. The third and fourth upper premolars of *C. horsfieldi minor* do not prove to be broader than those of *C. harpax*. The type skull of *C. harpax* is damaged, the rear of the skull including most of the braincase missing : the right ramus includes only the third and fourth premolars together with the

first and second molars, while the left ramus is represented by a fragment containing only the third and fourth premolars with the first molar. Nevertheless, there appears to be no size difference between *C. harpax* and *C. horsfieldi minor*, and no other characters can be found to separate them. They are therefore considered synonymous. Cranial measurements of *C. harpax* and *C. horsfieldi minor* from Sumatra and Malaya are compared in Table 1, while detailed measurements of the teeth of these forms are compared in Table 2. The length of the forearm of the type of *C. harpax* (measured from the dry skin) is 69·5.

The bat referred to in this paper as *Cynopterus horsfieldi minor* (Lyon) is currently called *Cynopterus horsfieldi lyoni* Andersen (Chasen (1940)). The earliest name applied to the Horsfield or larger dog faced fruit-bat (*Cynopterus horsfieldi*) of Sumatra is *Niadius minor* Lyon (1908). Lyon followed Miller (1906) in considering *Niadius* generically distinct from *Cynopterus*. Subsequently, Andersen (1912), following the lead of Thomas and Wroughton (1909) who considered *Niadius* at most a subgenus of *Cynopterus*, reduced *Niadius* to the synonymy of *Cynopterus*, admitting only a *Niadius* section. *Cynopterus minor* (Lyon) he therefore considered a secondary homonym of the combination *Cynopterus* (*Cynonycteris*) *minor* used by Trouessart (1878) (actually equal to *Rousettus minor* (Dobson)) and he proposed *Cynopterus horsfieldi lyoni* as a substitute name. Subsequent work has shown the Malayan representative of *C. horsfieldi* to be identical with that from Sumatra. Furthermore, *Cynopterus harpax* Thomas and Wroughton from Malaya proves to be synonymous with *C. horsfieldi* from Sumatra and Malaya. The question arises as to the correct name and synonymy of this bat.

The London meeting in 1958 of the International Congress of Zoology ruled that secondary homonyms are not to be permanently rejected. Since the

Table 1—Cranial measurements of *Cynopterus horsfieldi minor* and *Cynopterus harpax*.

	Cynopterus horsfieldi minor. Sumatra (Five skulls except where stated)	Malaya (Six skulls except where stated)	*C. harpax*. Type 8.7.20.7.
Greatest length	32·3–34·1 (32·8)	32·9–35·1 (33·8) (five skulls)	—
Condylobasal length	30·5–32·7 (31·1)	31·5–33·3 (32·4) (five skulls)	—
Palatal length	16·5–17·8 (17·0)	16·4–18·1 (17·4)	17·6
Orbit-nares	6·5– 7·4 (6·9)	6·6– 7·8 (7·2)	6·7
Zygomatic width	22·0–23·2 (22·6)	22·3–24·5 (23·4)	—
Interorbital width	5·5– 6·6 (6·1)	5·6– 6·8 (6·1)	5·6
Postorbital width	5·3– 5·8 (5·5)	5·6– 7·5 (6·4)	5·5
Braincase width	13·5–14·7 (13·9)	13·8–15·0 (14·4) (five skulls)	—
m^1–m^1 (alveoli)	9·7–10·4 (10·0)	9·7–11·0 (10·2)	10·0
c–c (alveoli)	6·8– 7·0 (6·9)	6·6– 7·4 (7·1)	—
c–m^1 (alveoli)	10·2–11·2 (10·8)	10·4–11·2 (10·8)	10·5
c–m_2 (alveoli)	11·5–12·7 (12·1) (four skulls)	11·6–12·7 (11·2)	—

Table 2—Measurements of premolar and molar teeth of *Cynopterus horsfieldi minor* and *Cynopterus harpax*.

	C. horsfieldi minor. (Nineteen skulls)	*C. harpax.* Type 8.7.20.7.
p^3 width	1·7–1·9 (1·8)	1·8
p^4 width	1·7–2·0 (1·8)	1·8
m^1 width	1·6–1·8 (1·7)	1·7
p_3 anterior width	1·6–2·0 (1·8)	1·7
p_3 posterior width	1·6–1·9 (1·7)	1·6
p_4 anterior width	1·6–2·0 (1·8)	1·9
p_4 posterior width	1·5–1·9 (1·7)	1·7
m_1 anterior width	1·5–1·9 (1·7)	1·8
m_1 posterior width	1·4–1·7 (1·6)	1·6

combination *Cynopterus* (*Cynonycteris*) *minor* used by Trouessart refers to the species now called *Rousettus minor* (Dobson), there is no conflict between it and *Cynopterus horsfieldi minor* (Lyon), (1908), which becomes the valid name for the Horsfield fruit-bat of Sumatra and Malaya. *Cynopterus harpax* Thomas and Wroughton, (1909), and the substitute name *Cynopterus horsfieldi lyoni* Andersen, (1912), fall into its synonyny.

MEGAEROPS ECAUDATUS (Temminck)

1837 *Pachysoma ecaudatum* Temminck, Mon. Mamm. **2** : 94. Padang, west Sumatra.

Pahang : ♀♀ 60.731–737 (skulls extracted) Mount Brinchang, Cameron Highlands, 5,500–6,600 ft.

All specimens in alcohol.

The genus *Megaerops* was hitherto represented in the collections of the British Museum (Natural History) by three specimens, from North Borneo, the Malay Peninsula and Annam respectively. Despite its comparatively wide range, from Borneo and Sumatra to Annam, *Megaerops* appears to have been collected but rarely and there are few published references to it. This series of seven from Pahang form a valuable accession and present an opportunity to record detailed measurements of this little known bat. The type locality is Padang, west Sumatra, not the Malay Peninsula as stated by Osgood (1932). Ellerman and Morrison-Scott (1951) ascribe the Annamese record to Osgood (1932). As Osgood acknowledges, the genus was first recorded from Annam by Thomas (1927).

Measurements of seven specimens (except where stated) from Pahang : length of forearm 50·5–57·0 (54·5), greatest length of skull 25·6–27·7 (26·7), condylobasal length 24·7–26·3 (25·6) (six skulls), palatal length 13·3–14·0 (13·7) (six skulls), zygomatic width 17·1–17·9 (17·6) (six skulls), interorbital width 5·0–6·0 (5·6), postorbital width 5·1–6·7 (6·1), braincase width 11·2–12·3 (11·8), m^1–m^1 7·9–8·2 (8·0), c–c 5·0–5·5 (5·3), c–m^1 7·8–8·3 (8·0), c–m_2 8·7–9·2 (9·0) (all tooth measurements made at the alveoli).

DYACOPTERUS SPADICEUS (Thomas)

1890 *Cynopterus spadiceus* Thomas, Ann. Mag. nat. Hist. (6) **5** : 235. Baram, Sarawak.

Selangor : ♂ 60.738 (skull extracted) Ulu Langat Forest Reserves, Kajang. Specimen in alcohol.

This specimen is the first record of *Dyacopterus* from the Malay Peninsula and is the third known example of the genus, which hitherto was represented only by the type specimens of *D. spadiceus* and the Sumatran *D. brooksi* (described by Thomas (1920)), both in the collections of the British Museum (Natural History). The Malayan specimen is referred to *D. spadiceus* largely on account of its dentition, which resembles that of the Bornean form, with short incisors, low premolars and well developed posterior basal ledges on the maxillary teeth. No reliable estimate of colour can be made from the spirit specimen, but the head apparently is not darker than the back, resembling *D. brooksi* in this respect. In the majority of its dimensions the specimen is intermediate in size between *D. spadiceus* and *D. brooksi* ; the interorbital region is narrower than in the smaller *D. spadiceus* while the zygomatic width of the Malayan specimen exceeds that of the larger *D. brooksi*. Measurements of this specimen are compared with those of the type specimens of *D. spadiceus* and *D. brooksi* in Table 3. While no reliable taxonomic conclusions can be drawn from the small number of specimens available, it seems likely that *D. brooksi* from Sumatra, listed as a species by Chasen (1940), warrants no more than subspecific distinction from the Bornean form D. *spadiceus*.

Table 3—Measurements of *Dyacopterus spadiceus* and *Dyacopterus brooksi*.

	D. spadiceus.		*D. brooksi.*
	Type ♀ 90.1.28.4. Sarawak.	♀ 60.738. Malaya.	Type ♂ 20.1.15.1. Sumatra.
Forearm	77·5*	81·5	81·0
Greatest length of skull	—	37·1	39·6
Condylobasal length	—	34·8	37·1
Palatal length	18·9	19·5	20·2
Orbit-nares	7·7	7·9	9·0
Zygomatic width	24·8	27·6	27·0
Interorbital width	7·6	7·2	8·6
Width over postorbital processes	13·6	14·8	15·4
Postorbital width	5·8	6·3	6·7
Braincase width	—	15·9	16·3
Mastoid width	—	15·2	15·9
m^3–m^1 (alveoli)	10·9	11·3	11·6
c–c (alveoli)	7·5	7·9	8·5
c^1–m^1 (alveoli)	12·6	12·8	13·7
c–m_3 (alveoli)	15·5	15·4	15·9

* Signifies from dry skin

BALIONYCTERIS MACULATA (Thomas)

1893 *Cynopterus maculatus* Thomas, Ann. Mag. nat. Hist. (6) **11** : 341. Baram, Sarawak.

1921 *Balionycteris maculata seimundi* Kloss, J. Fed. Mal. St. Mus. **10** : 229. . Junction of Tahan and Teku Rivers, at the foot of Gunong Tahan, Pahang, Malaya.

Selangor : ♂ 60.739 (skull extracted), ♀♀ 60.740–746 (skulls extracted), 60.747–758 Bukit Lagong Forest Reserves, Kepong.

All specimens in alcohol.

Hitherto represented in the collections of the British Museum (Natural History) by the type specimen of *Balionycteris maculata maculata*, a co-type of *B. m. seimundi* and four specimens from Sarawak. Kloss (1921) separated a Malayan race *B. m. seimundi* from *B. m. maculata* of Borneo on the grounds that specimens from Borneo had their postorbital processes " much less developed : short and obtuse instead of pointed and elongated ". He apparently lacked specimens from Borneo when preparing the description of *B. m. seimundi* and refers to the figure of the skull of *B. m. maculata* in Andersen (1912), making no direct comparison of the two forms. The degree of development of the postorbital processes varies with the age of the specimen and is unreliable as a taxonomic character. A young adult male, 60.739, from Malaya, has relatively undeveloped postorbital processes : other specimens, rather older, show a greater degree of development while fully adult specimens from Malaya such as two females, 60.742–743 and the male co-type of *B. m. seimundi*, 26.10.19.2, have well developed processes terminating in a blunt point. A similar variation is demonstrated by the Bornean specimens examined : the male type of *B. m. maculata*, 93.4.1.24 and male 94.9.29.3, both old adults, have greatly developed pointed processes. Three younger female specimens, 93.4.1.25–27, resemble those of similar age from Malaya exactly. Apart from the co-type of *B. m. seimundi*, no adult male from Malaya is available but a comparison of the Bornean series with adult Malayan females suggests that the postorbital processes of males tend to be more pointed and more greatly developed than those of females. Kloss offered no other characters for the definition of *B. m. seimundi*.

The type specimen of *B. m. maculata* is in alcohol as is this further Malayan series, and some colour change has obviously taken place. However, the co-type of *B. m. seimundi* is a dry skin and the collections also contain dry specimens from Mt. Dulit, Sarawak (94.9.29.3) and Sarawak (93.4.1.27), the latter prepared from a spirit specimen. Comparison of this material reveals no taxonomically significant colour differences between Bornean and Malayan specimens. The spirit series, when dried, suggests that the extent of drab white tipping of the brown ventral pelage in *B. maculata* is variable, some specimens having the belly covered with brown hairs with white tips while in others most of the tipping is absent. In view of these conclusions, *B. m. seimundi* is reduced to the synonymy of *B. maculata*.

Measurements of seven female specimens from Selangor : length of forearm 40·6–42·1 (41·3), greatest length of skull 21·1–22·1 (21·8), condylobasal length 19·8–21·5 (20·7), palatal length 10·5–11·2 (10·9), zygomatic width 13·9–14·6 (14·4), interorbital width 4·3–4·9 (4·6), postorbital width 4·7–5·5 (5·1), braincase width 9·5–10·0 (9·8), p^4–p^4 5·9–6·6 (6·3), c–c 4·3–4·9 (4·5), c–m^2 6·8–7·2 (7·0), c–m_2 7·2–7·6 (7·4).

AETHALOPS ALECTO ALECTO (Thomas)

1923 *Aethalodes alecto* Thomas, Ann, Mag. nat. Hist. (9) **11** : 251. Indrapura Peak, Sumatra, 7,300 ft.

Pahang : ♂♂ 60.859–860 (skulls extracted), ♀♀ 60.861–863 (skulls extracted) 60.864 Mount Brinchang, Cameron Highlands, 5,500–6,600 ft.

All specimens in alcohol.

These specimens of *Aethalops* are the first to be recorded from the Malay Peninsula. The genus was hitherto represented in the collections of the British Museum (Natural History) by a single specimen, the type of *A. a. alecto*. It also occurs in Borneo, whence G. M. Allen (1938) described a second form *A. aequalis*, from Mount Kina Balu, 5,500 ft., here considered to be a subspecies of *A. alecto*. The following notes on colour are based on three Malayan specimens which were collected in February, 1960 and which had been immersed in alcohol for three months at the time of examination. In two males the dorsal colour is grey black, the hairs with dark grey bases. The dorsal surface of the head is the same colour as the back. The underside of the body is slightly paler, the hairs tipped with silvery grey. A female specimen is browner on the back but retains the dark head. Its underside is browner, lacking much of the silvery grey tipping. It agrees closely with the description of *A. a. aequalis* : as in that race the upper half of the humerus, a strip along the sides of the body, the upper surface of the hind leg to the base of the claws and the interfemoral membrane are a clearer brown than the darker central area of the back. These observations are confirmed by two other female specimens from Malaya, which at the time of examination had been in alcohol for twelve and eighteen months respectively. In both male and female specimens a few very inconspicuous lighter spots are to be found on the wing membranes. Cranially, Malayan specimens are very similar to the type specimen of *A. a. alecto*. As in the type specimen, the inner upper incisors are smaller and shorter than the outer pair but the braincase is broader and more inflated and the interorbital and postorbital regions wider than in the type. More Sumatran material is needed, however, to evaluate this variation. Thomas gave no skull measurements for the type specimen of *A. a. alecto*. These, together with those of the Malayan series, appear in Table 4.

Aethalops alecto aequalis differs from *A. a. alecto* in that the inner upper incisors are equal in height to the outer upper incisors, while in *A. a. alecto* they are shorter than the outer pair. No inconspicuous lighter spots are to be found on the wings of *A. a. aequalis*. The colour of female specimens from

Table 4—Measurements of *Aethalops alecto alecto*.

	Type ♀ 23.1.2.1. Sumatra	Malaya (four specimens)
Forearm	47·0	44·5–47·5 (45·6)
Greatest length of skull	24·5	24·2–25·4 (24·9)
Condylobasal length	23·3	23·2–24·4 (23·7)
Palatal length	12·2	12·0–13·0 (12·6)
Zygomatic width	15·3	14·9–16·4 (15·7)
Interorbital width	4·8	5·3– 5·6 (5·5)
Postorbital width	5·2	6·1– 6·4 (6·3)
Braincase width	10·2	10·7–11·1 (10·8)
Mastoid width	10·2	10·4–10·7 (10·5)
p^4–p^4 (alveoli)	7·3	7·2– 7·6 (7·4)
c–c (alveoli)	4·8	4·7– 4·9 (4·8)
c–m^1 (alveoli)	7·4	7·5– 7·8 (7·7)
c–m_3 (alveoli)	8·3	8·3– 8·6 (8·4)

the Malayan series, referred to *A. a. alecto* on dentition and size, agrees closely with the description of *A. a. aequalis*, which was based on a female specimen (G. M. Allen (1938)), together with three female paratypes (G. M. Allen & Coolidge (1940)). *Aethalops a. alecto* has a slightly larger skull than the type specimen of *A. a. aequalis* but Malayan specimens of *A. a. alecto* have the forearm shorter than that of the Sumatran type and equal in length to that of *A. a. aequalis*. Comparison of the meticulous description of *A. a. aequalis* by Allen with the type specimen of *A. a. alecto* and a series from Malaya reveals no other differences of taxonomic significance, and the existing differences are not thought to justify the retention of specific rank for *A. a. aequalis*.

CHIRONAX MELANOCEPHALUS (Temminck)

1825 *Pteropus melanocephalus* Temminck, Mon. Mamm. **1** : 190. Bantam, west Java.

Selangor : ♂♂ 60.865 (skull extracted), 60.871, ♀♀ 60.866–870 (skulls extracted), 60.872–878 Bukit Lagong Forest Reserves, Kepong.

All specimens in alcohol.

This bat, rare in collections, was hitherto represented in the British Museum (Natural History) by a single specimen, from Nias Island, off the west coast of Sumatra. Chasen (1940) also records it from north Sumatra and Selangor, Malay States. This series, which at the time of examination had been preserved in alcohol for seven to ten years, is of little use for colour study. Despite obvious loss of colour, the specimens have the characteristic darker head and both male and female specimens occasionally exhibit a patch of bright orange at the sides of the throat just anterior to the shoulder. The length of the forearm in twelve specimens is 42·5–47·5 (45·5).

Measurements of six skulls (except where stated) : greatest length 23·0–23·7 (23·4), condylobasal length 22·0–23·0 (22·5), palatal length 11·8–12·2 (11·9), zygomatic width 15·0–15·7 (15·3), interorbital width 4·7–5·3 (5·0), postorbital width 5·2–5·9 (5·6), braincase width 10·0–10·6 (10·2), p^4–p^4 6·6–7·1 (6·8), c–c 4·2–4·8 (4·5), c–m^1 7·1–7·5 (7·3), c–m_2 8·2–8·7 (8·4) (five skulls) (all tooth measurements made at the alveoli).

PENTHETOR LUCASI (Dobson)

1880 *Cynopterus* (*Ptenochirus*) *lucasi* Dobson, Ann. Mag. nat. Hist. (5) **6** : 163. Sarawak.

Selangor : ♂♂ 60.751–785, ♀♀ 60.786–837 Bukit Lagong Forest Reserves, Kepong. ♂♂ 60.838–848, ♀♀ 60.849–858 Ulu Langat Forest Reserves, Kajang.

Pahang : ♂ 60.929, ♀ 60.930 (both skinned from alcohol, September, 1960, with skulls) Mount Brinchang, Cameron Highlands, 6,600 ft.

All specimens in alcohol unless stated.

Two specimens, 60.929–930, collected in September–October, 1959 from the high slopes of Mount Brinchang, Cameron Highlands, Pahang, are appreciably darker than skins of *Penthetor lucasi* from the lowlands of the Malay Peninsula. At the time of examination, they had been in alcohol for ten months. Dorsally, they are very dark, the grey based hairs with black or seal brown tips, those over the shoulders less densely tipped, allowing more of the grey base to appear. The nape and the top of the head are the same colour as the back. The dorsal brown of lowland specimens in these montane

examples is replaced by black or darker brown. The ventral surface of the montane specimens is pale brownish grey, the brown based hairs with grey or grey white tips. These specimens, darker dorsally and more grey ventrally than those from the lowlands of the Malay Peninsula, suggest the existence of a montane race of *P. lucasi* in the central Malayan highlands.

SUMMARY

This paper describes a number of hitherto poorly known Malayan Megachiroptera, with notes on their taxonomy. Variation in *Cynopterus brachyotis* from the south-east Asian mainland is studied and a montane race, *C. b. altitudinis*, is described as new. *Cynopterus horsfieldi minor* (Lyon) is considered the valid name for the Horsfield fruit-bat of Sumatra and Malaya. *Cynopterus harpax* Thomas and Wroughton is reduced to the synonymy of *C. horsfieldi minor*. *Dyacopterus spadiceus* and *Aethalops alecto alecto* are recorded for the first time from the Asiatic mainland. *Dyacopterus brooksi* from Sumatra is thought to be a race of *D. spadiceus* and *Aethalops aequalis* from Borneo is considered a race of *A. alecto*. *Balionycteris maculata seimundi* Kloss is made a synonym of *B. maculata*, which is considered to be monotypic.

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NOTICE

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